

# A STATISTICAL STUDY OF THE RATTLESNAKES

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78,652

## VI FANGS



### Introduction

The length and character of the fangs of the rattlesnake present a study of some practical interest, since they involve several of the variables which affect the results of snake-bite, as, for instance, the depth of penetration of the venom, the rapidity of injection, the amount of venom which may be lost externally in clothing, and the chance of fang breakage in contact.

When one extracts venom from rattlesnakes of different species, it is at once apparent that the fang lengths, while roughly proportional to the body sizes, exhibit differences in this proportionality between species. There can be no doubt, for example, that the fangs of a Crotalus tigris are much smaller than those of a C. molossus of similar body size. But the heads of these snakes are likewise disproportionate and it might therefore be assumed that the fang lengths have a fixed relation to head size. Upon investigation, however, it appears that such is not the case either; there are also differences in the fangs when the head sizes are equal. The determination of the relationship between these body parts is one of correlation, which can best be attacked by statistical methods. It involves, as usual, a preliminary study of the extent of intraspecific variation and dispersion, followed by interspecific comparisons. However, before this is undertaken, there are several features of the fangs and their use which should be discussed, since their presentation will clarify the application of the measurements upon which the statistical studies are based. Of particular interest are the highly specialized mechanisms of fang replacement and of fang operation. Regarding them, certain conflicting descriptions have appeared in the past, and these I will seek to correct and amplify.

### Fang Growth and the Mechanism of Replacement

It is well known that the active fangs of the rattlesnakes are changed or replaced periodically, such renewal occurring whether the discarded member has been damaged or is still intact. Whether replacement is hastened, if a functional fang has been broken out entirely, prior to the normal time of change, is not known. The delicacy and fragility of the fangs, particularly in the smaller snakes, makes such a provision for replacement imperative, as does likewise the necessity for providing larger fangs as a snake grows.

The mechanism whereby a new active fang comes into position has been described by several investigators; over sixty years ago two mutually exclusive descriptions were formulated, both of which have subsequently reappeared in the literature from time to time. It is desired here to point out the difference between these theories of develop-

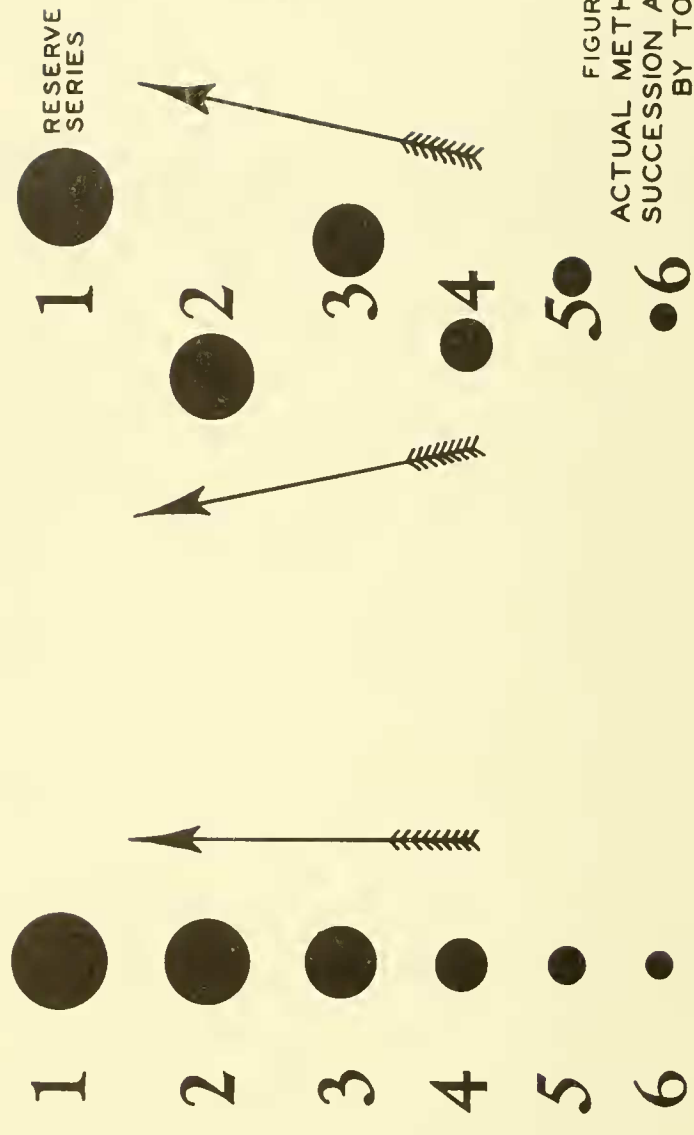


FIGURE 17  
MITCHELL'S THEORY OF  
FANG SUCCESSION

FIGURE 18  
ACTUAL METHOD OF FANG  
SUCCESSION AS OBSERVED  
BY TOMES

*Note: The separation between maxillary sockets is only for diagrammatic clarity; Actually they touch each other.*

ment and to present a statistical verification of one of them.

Dr. S. Weir Mitchell, the celebrated neurologist, ophiologist, and author, and a collaborator, Dr. Christopher Johnston, were the first to describe in detail the mechanism of change.\* They state that on each side of the head there is a pair of contiguous maxillary fang sockets, making four sockets in all. Posterior to the inward socket of each pair lies a magazine holding the future fangs in an ascending order of size and completeness (Fig. 17). Of the two sockets, the outer usually holds the active fang, the inner being normally vacant. When the time of replacement arrives, the forward reserve fang, which is also the largest and most fully developed, advances and becomes firmly seated in the vacant inside maxillary position on that side of the head. The old outer fang drops out, whereupon the new fang moves laterally to a permanent position in the outer socket, leaving the inner once more vacant. Thus the inner socket is used only during the transition period, the outer being the regular location of the functional fang.

Charles S. Tomes,<sup>†</sup> on the other hand, pictures the two sockets as being used alternately to hold the active fang, the immature fangs being contained in a magazine in a staggered line behind the two sockets, the most mature of the reserve series being always behind the vacant socket (Fig. 18). When the time for a change arrives, this fang advances to the vacant socket anterior to it and becomes seated permanently therein. The superseded fang drops out, leaving a vacant socket, to which, in due course, the next replacement advances. Thus, according to Tomes, the active fangs are alternately in the inside and the outside positions.

An examination of a number of specimens, and the compilation of some statistics with respect to fang positions, show conclusively that Tomes' description is correct, and that the Mitchell theory should be discarded.

In every normal rattlesnake there will be found two fully formed fangs on each side of the head, in addition to the less mature members of the replacement series. When the protective sheath has been cut away to expose these two, one, the active or functional fang, will be found firmly fixed in its maxillary socket; the other is the first reserve fang and is nearly always loose, that is, with its base unanchored to any part of the skull. Upon examining a considerable number of snakes, these first reserves are found in all stages of development, from being imbedded in their native capsules, to fully-advanced to the maxillary position, but not yet firmly seated.

I have described these two fangs, on a side, as being fully formed or complete. This is true of the fangs proper, but not of their bases. One, the presently func-

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\* S. Weir Mitchell: Researches upon the Venom of the Rattlesnakes. Smithsonian Contributions to Knowledge, Vol. 1, pp. 16-29, 1861.

<sup>†</sup> Charles S. Tomes. On the Development and Succession of the Poison-fangs of Snakes. Philosophical Transactions, Vol. 166, pp. 377-385, 1877.

tional fang, is anchored solidly in its maxillary socket upon a bony base, or pedestal. The other, the reserve which will shortly replace it, has a softened immature base. The degree of hardening of this base corresponds to the closeness of approach of the first reserve to its socket. Sometimes the first reserve is still grouped with the other, less mature reserves; again it may be found in a later stage of development, that is, advanced to the maxillary position, and with the base somewhat hardened, so that, as the maxillary is tilted, the reserve tends to rise also, just as does the fully functioning fang. When in this condition, the reserve can still be distinguished from the fang it is about to replace by a slight looseness at the base, evident as the fang is manipulated with a forceps.

Rarely, both of the two fangs on a side are found to be firmly set in their respective maxillary sockets, that is, at the exact interval when the new fang is fully functioning and the older has not yet dropped out. This occurs so infrequently, however, that we know this period of overlap must be rather short, compared with the time between fang changes. On the other hand, so seldom is a functional fang missing and the first reserve not yet in place, that we know an overlap, i.e., an interval with two functional fangs on a side, though short, must be the normal sequence. The absence of a functional fang on one side can no doubt be construed to be the result of some mishap incident to capture; certainly this is not a condition representing a normal sequence in replacement.

In choosing between the two processes of change, as described by Mitchell and Tomes, it is important to observe, first, that dissection shows the advancing first reserve to be always behind the vacant maxillary socket, which is just as likely to be the outer as the inward cavity. The Mitchell theory would require the advancing fang to be always behind the inner position, and that fixed fangs should be found in a transition stage, moving from the inside to the outside socket. Neither of these conditions is verified.

In an examination of 210 specimens of rattlesnakes of various species, fangs were found functional in the inside location in 205 of the 420 cases, while the outside socket was occupied by the active fang in 215 cases. This shows that there is an equal usage of the two sockets for the location of the functional fang; certainly it is far from indicating that the outside position is the sole functioning locality except during the transition stage.

A section discloses the fact that the future fangs lie, not in a single row as pictured by Mitchell (Fig. 17), but in two alternating rows as stated by Tomes (Fig. 18). Between these rows there is a heavy, protecting wall of tissue, of greater thickness than that which separates each succeeding fang from its fellow on the same side; thus it is impossible for one of the inner series to reach the outer maxillary socket or vice versa. This dividing wall is maintained between the fangs even when, for a short time, there are two functional fangs on a side. The wall is not joined to the sheath anterior to the fangs.

Another objection to the Mitchell theory is the difficulty entailed in holding the fang and keeping it

active while in the transition stage between the inner and outer sockets, particularly as a ridge intervenes, so that a fang would have to be lifted partly out of the socket in order to move laterally. Furthermore, the fangs of the two series are slightly asymmetrical; they are not equally suited to either socket, a detail to which reference will again be made.

Thus by the examination of a number of specimens showing the fangs in all positions, and by statistics and dissection, we have a view which is equivalent to seeing the process in motion; and there is no question concerning the alternating use of the inner and outer maxillary sockets to hold the active fangs.

There appears to be no synchronism in the advancement of the fangs on the two sides to their functional positions. Thus, of 210 specimens, 111 had an asymmetrical arrangement, with one inside and one outside socket in use. In the other 99 cases the functional fangs were either both in the outside, or both in the inside positions, there being 52 with both outsides functional and 47 with both insides. This indicates that the entire arrangement is one of chance; that, in general, half of the cases should be asymmetrical; and, of the remaining half, the pairs should be equally divided between inside and outside positions. Even in a group of specimens recently born, neither symmetry nor a definite tendency toward the inside or outside position could be detected.

The statistical data here given are the result of an examination of specimens of the two rattlesnake genera, Crotalus and Sistrurus. A study of a few individuals of the other genera of the Crotalidae, the family of the pit-vipers, Bothrops, Trimeresurus, Lachesis, and Agkistrodon, indicates the employment of the same mechanism. Since Tomes' investigation included Vipera it is evidently the mechanism of the Viperidae also.

The separation of the two sockets on each side is just sufficient to provide an anchorage for each fang, and to prevent interference during the short interval when both contain active fangs. The inside socket is a short distance anterior to the outside. In describing arcs, when erected, the two fangs on a side tend to swing toward the same point, so that the separation of the puncture points of a bite is not appreciably greater with two outside than two inside fangs. This is shown by the fact that when two active fangs are found on a side, the lateral clearance between the points is usually less than the center-to-center separation of the sockets. However, one point may be advanced ahead of the other.

In a large Crotalus cinereous, using the head length as a basis equal to 100 per cent, we find the fangs to be situated posterior to the rostral by about 18 per cent. The separation of the outer sockets is about 42 per cent of the head length and the inner sockets about 36 per cent. Thus the centers of two sockets on one side of the mouth are separated by about 3 per cent of the head length, and the head length is about  $2\frac{1}{2}$  times the fang separation. From data on head sizes (see Part V, this series)\*, a rough approxima-

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\* References to previous parts of this paper are cited by part number. The dates and numbers of the Occasional Papers of the San Diego Society of Natural History in which these parts appeared are given on the first page of this paper.

tion can be made of the size of a snake that has caused an injury, if the distance between the fang punctures and the species of snake be known; however, because the articulation of the erecting mechanism is such as to permit a considerable lateral play, there can be no great accuracy in this determination.

Even when still imbedded in the reserve sac, the distal section of the first reserve fang, from the middle of the upper orifice to the point, is fully hardened on the exterior and of full length; that is to say, the length will agree, to a fraction of a millimeter, with the length of the adjacent functional fang which it is about to replace. However, above the mid-point of the upper opening or lumen the process, or pedestal, which will later engage the socket, will be found to vary considerably in completeness, depending on the imminence of replacement. It is the solidification of this pedestal which anchors the fang in the socket.

From a study of the paired fangs on a side, in rattlers which are exactly at the time of fang change, that is, with both the new and old fangs firmly anchored, it is observed that the solidification of the pedestal has a considerable effect on the direction in which the fang points. Sometimes the two fangs are parallel, with the points almost touching each other, but often one of the points is advanced somewhat ahead of the other. Occasionally one fang may be crossed over the other. In an atypical case of a double-fanged adamanteus with fangs 17 mm. long, the outer fang point was 1.6 mm. ahead of the inner. The lateral clearance between points was 1.8 mm.; the center-to-center socket separation 3.0 mm. While the outer maxillary socket is always slightly posterior to the inner, and its bottom is not quite so deep, nevertheless these differences do not produce an invariable orientation of the two points. Much seems to depend on the position occupied as solidification in the maxillary takes place.

Looking at the first reserves in all degrees of advancement, it is found that if a long time is to intervene prior to replacement, the first reserve fang does not move if the maxillary is tilted. On the other hand, if replacement is imminent, the fang tends to rise as the maxillary is rotated, although it is not yet fixed. Finally, complete solidification in the socket takes place and then, when the maxillary is rotated, both the new functional fang, and the old fang about to be replaced, rise as a unit. Examination indicates that the posterior part of the bony pedestal or frustum solidifies last.

Snakes change their fangs so frequently, compared with the growth of head or body, that measurements do not ordinarily indicate a larger size of the first reserve fang, as compared with the functional fang it is about to succeed. Comparisons in several species as frequently showed the functional fang to be the longer of the two, as vice versa, except in a series of yearling Crotalus ruber. Here the growth was sufficiently rapid that the first reserve fang averaged nearly 0.1 mm. longer than the functional fang. No doubt the same situation would be found in other large species, such as lucasensis and cinereous, during adolescence, the period of fastest growth.

It is well known that the fangs of pit vipers,

such as the rattlesnakes, appear to be fabricated by rolling a flat section so as to form a solid tube, much as butt-welded pipe is made; for there is a sort of joint or suture, evidenced by a dark line along the front of the fang. Both lumens are really gaps in the suture, the upper or inlet opening being short and relatively wide, while the lower, or discharge orifice, is a long and narrow slit (Figs. 19, 20, and 21). As the two surfaces of the hypothetical flat member are both covered with dentine it follows that, after rolling or folding, the inner surface of the tube (the canal) is coated in the same way as the outer; however, the inner surface is considerably softer. The line of the longitudinal suture or weld can be clearly seen in the larger fangs, but so perfect is the joint that it cannot be felt with a sharp needle, except rarely near one of the apertures. The interior line of the joint is even more perfect, for it can be seen only with a magnifier under strong light. When a functional fang is broken, there is no tendency of the break to follow this line; yet it is a real suture, as shown by studies of immature fangs. The material of the fang is very brittle and shatters under strain. The surface can be cut with fine sandpaper or a file, or scratched with a needle point. The surface of the tip of the fang seems slightly harder than the upper parts.

The growing fangs are developed or completed, not as a unit, but from the point upward, the point being fully formed and hardened long before the upper part takes shape. Also, while the form of the fang indicates derivation from a flat plate rolled into a tube, the actual growth does not proceed in this manner; for, from the earliest period of development in which the form can be ascertained, the tubular shape is in evidence.

The development or growth can best be explained by describing a typical series. For this purpose the following notes were made on an adult C. cinereus having a head length of 56 mm. It should be understood that this description covers the mechanism on one side of the head only, in this case the left. Reference is also made to Fig. 22.

(1) The functional fang is in the outside socket, being solidly anchored therein upon a striated pedestal of bone. The tube is translucent and the canal clear. Breakage, by inserting a needle in the lower aperture, causes shattering, but the cracks do not follow the longitudinal joint or weld. The straight line distance from the lower end of the upper lumen to the point is 12.2 mm.

(2) The first reserve fang is at the head of the inside series. It is well advanced toward the inside maxillary socket, but has not yet reached its final forward position. It is loosely held. The fang seems finished and hardened from the point to the central part of the upper lumen; above this, the section which will later be imbedded in the maxillary socket, i.e., the bony pedestal, is quite soft. The base, as far as completed, is hollow; this hollow (the pulp cavity) does not communicate with the venom canal or duct. The latter is partly filled with what is evidently nurturing tissue. The upper-lumen-to-tip length is 12.2 mm., or the same as in the functional fang. Insertion of a needle point in the lower aperture shatters the fang, and the breakage partly follows the longitudinal weld.

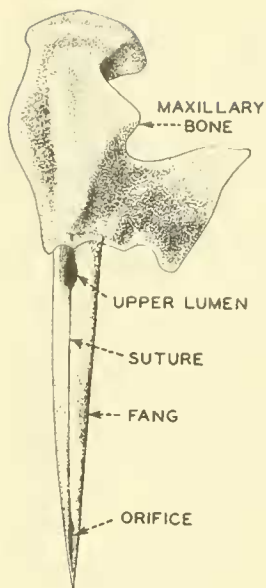


FIGURE 19  
FANG IN INSIDE  
MAXILLARY SOCKET

*(The orifice appears foreshortened because of the direction of the joint below the central arc.)*

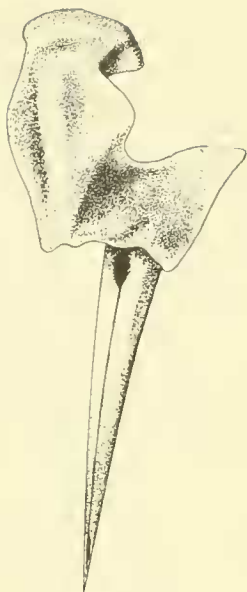


FIGURE 20  
FANG IN OUTSIDE  
MAXILLARY SOCKET

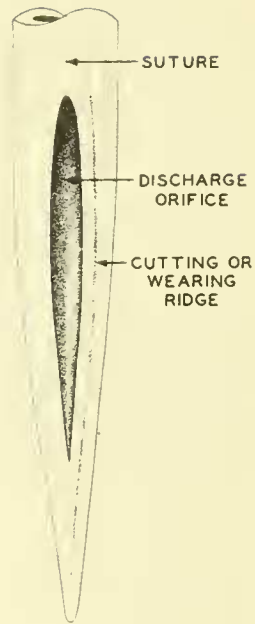


FIGURE 21  
PERPENDICULAR VIEW  
OF POINT OF FANG



FIGURE 22  
RELATIVE COMPLETENESS OF SERIES OF DEVELOPING FANGS

*First replacement fang is at the left; youngest and on the right. Solid parts are calcified; dashed sections formed but uncalcified; dotted sections unformed.*



(3) The second reserve (outside position) fang is complete only to the lower tip of the upper lumen. It is hard at the point but pliable above. The surface is polished and fairly translucent. The length of the complete section is 11.8 mm. The lower lumen appears perfect and of full size. Insertion of a needle point, however, shows the material to be somewhat pliable, and the longitudinal weld opens quite easily and regularly. This and the subsequent fangs are closely surrounded by capsules of tissue and the tubular interiors are filled with tissue.

(4) Third reserve fang (inside). The lower end of the fang is complete but slightly pliable; the upper end is quite soft and the entrance lumen has not begun to form. The lower, or discharge aperture, seems to be perfectly formed and of full size; the point, however, is dull, not sharp as in a completed fang. The length over-all is 10.1 mm. The tubular form is as perfect as in a functional fang; the longitudinal weld is clearly to be seen, but cannot be felt with a sharp needle. However, the introduction of the needle point into the lower aperture causes the suture to separate readily.

(5) Fourth reserve fang (outside). This fang is soft at the top; however, the lower lumen is quite completely formed, although pliable. The point is dull, thereby showing incompleteness. The exterior, when stripped of the capsule, is shiny and transparent. The length is 7.0 mm., of which only 2.2 mm. are above the upper end of the lower lumen.

(6) Fifth reserve fang (inside). There is nothing above the upper end of the lower aperture; below, the fang is of full size, and rather firm. The point is dull. The length is 4.8 mm.

(7) Sixth reserve fang (outside). A dull point and the lower end of the lower lumen are to be seen, and are moderately firm. Such part of the lower orifice as is in evidence has a crescent-shaped cross section, not flat; the ultimate form can be clearly recognized.

(8) Seventh reserve fang (inside). This is only a small conical shape attached to the magazine wall; it is evidently the future capsule, the fang not being recognized.

The facts most forcibly brought to attention by the examination of this series are: first, that if the fang were originally developed from a partly folded, and thus grooved, tooth, the process is not at present repeated in the growth of the individual fangs. Secondly, the fangs do not grow by the enlargement of their parts; on the contrary, the first stage is the development of the fang in its full size in the vicinity of the lower aperture, followed by the completion of the point and then the gradual extension of the upper section. If there is a suggestion of derivation from a grooved fang in the present suture or weld, and the continuity of the external dentine surface with the internal surface of the canal, it is no longer evident in the development of the tubular section of an individual fang, at least prior to the deposition of dentine. The only resemblance to a grooved fang, during the present method of individual fang growth, lies in the appearance of the lower aperture during its formation. This is the part of the fang first formed,

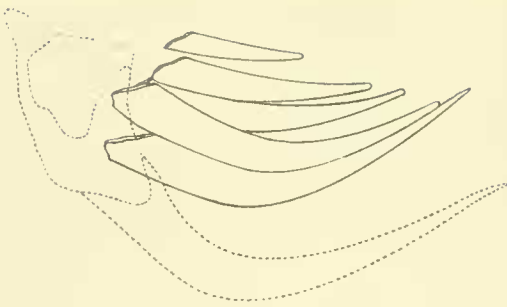


FIGURE 23  
LOCATION OF REPLACEMENT SERIES

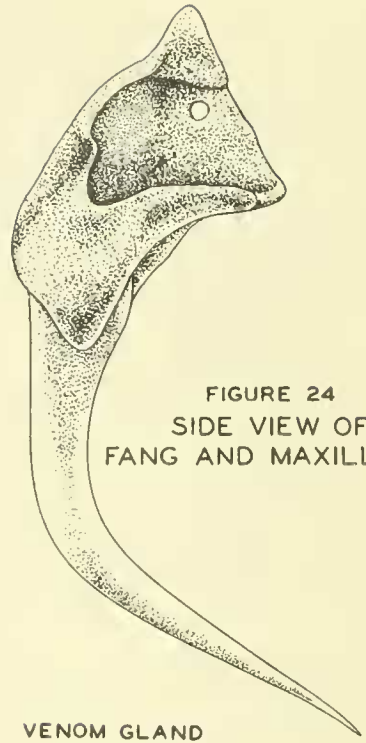


FIGURE 24  
SIDE VIEW OF  
FANG AND MAXILLARY

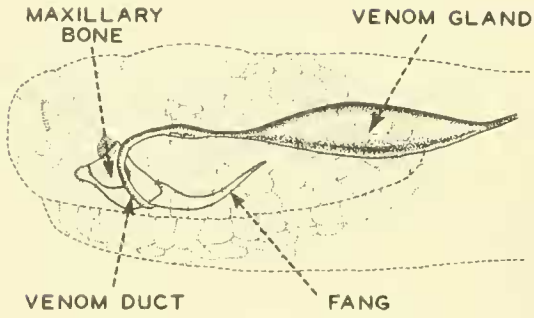


FIGURE 25  
RELATIVE POSITIONS OF  
VENOM GLAND, DUCT, AND FANG

and, as the aperture is in reality a deep slot, we have, in effect, a short grooved tooth. To this the upper tubular section is subsequently added.

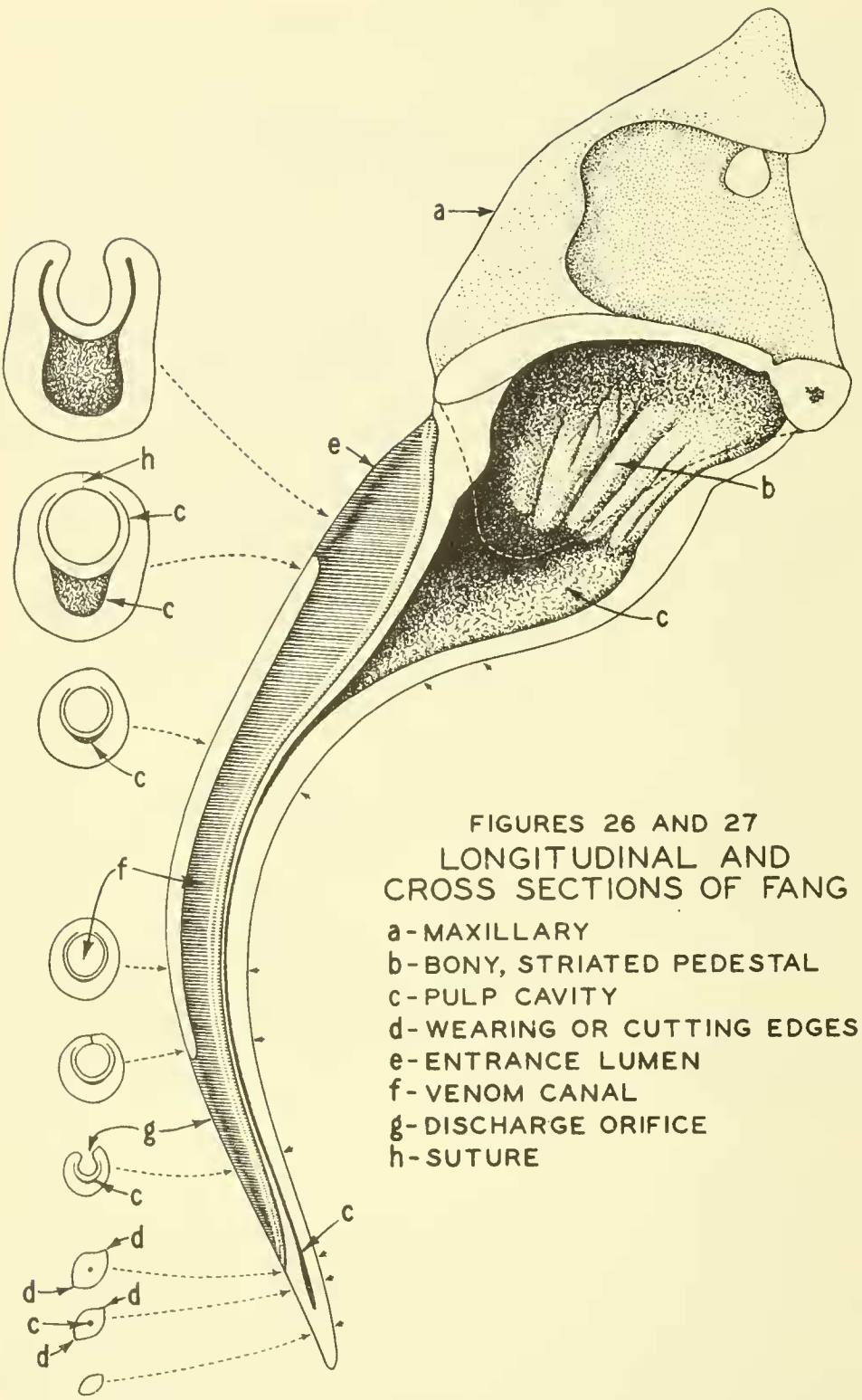
Little seems to be known concerning the normal frequency of fang change. Having noted the effect of captivity upon the frequency of exuviation, I am doubtful if we can learn much from observations on captive specimens. It is to be presumed that the final loss of the obsolescent fangs usually occurs in feeding. Discarded fangs are frequently found in the digestive tract. Dr. Charles A. Vorhies of the University of Arizona has shown clearly in motion pictures that C. cinereous, in feeding on rabbits, uses the fangs alternately to pull the prey into the mouth, just as a colubrine snake uses its mandibular teeth. This use would no doubt break off a fang about to be lost, just as certainly as striking prey or an enemy.

The method of removal of the functional fangs is not known with certainty. To judge from an examination of obsolete and defecated fangs, or observation when they are broken off in the venom-milking process, the fracture occurs close to the outer or distal edge of the maxillary socket, which is at the proximal end of the dentine area. This leaves a considerable amount of bony material (the pedestal) within the socket. Whether this drops out later, or is absorbed, I am not prepared to say; at least it is not retained for use with the next fang, since a resting maxillary socket is entirely vacant.

In the above discussion the reserve fangs have, for clarity, been described as lying behind the functional fang and advancing forward into position. Actually they lie rather above than behind, as shown in Fig. 23. They are not widely separated as in Fig. 18, for here they have been spread to indicate the order of succession; nor even to the extent shown in Fig. 23, wherein it was desired to illustrate the relative sizes and states of completion of the first five reserves. Instead, they are as closely crowded together in the reserve magazine as their dimensions and the surrounding capsules will permit. With the maxillary folded into its inactive position, the base of the first reserve lies opposite the socket in which it will be anchored. Solidification of the bony pedestal then takes place.

### Fang Structure

The shape of the functional fang is such as to preclude a simple description. It may be likened to a thin or slowly tapering cone, with a spreading or buttressed base, and with the central section bent into a circular curve, this curve describing an arc of from 60 to 70 degrees (Fig. 24). The basal tangent section is short and is of irregular shape, because of spreading to form the entrance lumen, and with a general reinforcement or abutment at the anchorage. This abutment surrounds the pulp cavity, which is greatly enlarged at the base. The reinforcement is largely secured by massing material posteriorly around the pulp cavity, with some lateral increase as well. In this, the two fangs on a side (whose alternating occupancy of the two maxillary sockets has been discussed) are slightly asymmetrical, the inner fang spreading inwardly, and the outer in the contrary direction. However, most of the asymmetry required by



FIGURES 26 AND 27  
LONGITUDINAL AND  
CROSS SECTIONS OF FANG

- a-MAXILLARY
- b-BONY, STRIATED PEDESTAL
- c-PULP CAVITY
- d-WEARING OR CUTTING EDGES
- e-ENTRANCE LUMEN
- f-VENOM CANAL
- g-DISCHARGE ORIFICE
- h-SUTURE

the dissimilar shapes of the two sockets is not provided by the fangs proper, but by the temporary pedestal structures of bone, whose difference from the fangs is evidenced by a discontinuity in the surface, these bony frustums having a duller and softer surface texture than the dentine covered fangs. The frustums are striated or corrugated for reinforcement; and, as some of the striations continue across the proximal parts of the dentine covered surface, a partial continuity with the fang is indicated. The pedestal frustums are irregularly shaped to engage the sides (rather than the bottoms) of the bony maxillary sockets; and, in this engagement, the asymmetry of the two sockets is largely compensated.

The tangent at the point of the fang is proportionately longer than the basal tangent. The former is produced, not only by the straightening of the axis of the cone, but by the elliptical opening of the discharge lumen as well. Often, especially in the larger specimens, there is a slight reverse curve in evidence at this point; this serves to prevent the fang, when in its resting position against the roof of the mouth, from being directed against the tissue (especially the venom gland) lying immediately above it (Fig. 25).

The canal within the fang tapers as does the outer section. A cross section shows the fang to be slightly elliptical, especially in the proximal section (Table 30). The walls are thickened opposite the major axis, as would be desirable from a structural standpoint; for the forces exerted in biting, striking, or drawing in prey, are likely to be in the plane of the curve. At the center of the curve of an adamanteus fang, having an upper-lumen-to-point length of 13.7 mm., the interior canal was found to measure about 0.7 by 0.8 mm., the walls being 0.25 mm. thick on the shorter axis, and 0.35 mm. on the longer, making the external dimensions 1.2 x 1.5 mm.

At the base of the fang the pulp cavity lying behind the venom canal, with which it has no connection, is of considerable size. There is an aperture in the rear of the basal pedestal giving access to the pulp cavity. The cavity, which has the effect of dividing the fang into a pair of tubes, one within the other, decreases in size distally until it practically disappears at the central curve, at which place only a vestige usually remains (Figs. 26 and 27). However, in large fangs it can be traced into the very point of the fang. The extent and location of the pulp cavity can best be ascertained by pinching off successive pieces of a well dried fang; the cavity can sometimes be followed by a discoloration between the interior and exterior tubes, which tend to shatter and separate along the pulp cavity surface. The inner tube is much thinner than the outer; its polish is not so high, and it is slightly softer. Often there is no space or color between the tubes, although they are still distinguished by a plane of separation. However, at the front, as the tubes approach the suture, they fuse into a homogeneous material. Toward the upper lumen the thin inner tube is completely separated from the outer by the pulp cavity, except at the front where, along the line of the one-time suture, the two are still fused. The relationship between the inner and outer tubes, and the pulp cavity, is best explained by a series of cross sections along the fang (Figs. 26 and 27).

On the larger fangs there can be seen a faint yellow ridge paralleling the lower aperture just beyond its outer edge, and extending from the point to a short distance above the upper end of the opening. The ridge is slightly roughened. There is a corresponding ridge on the under side of the point; as a result of these ridges the point has an elliptical cross section, with the major axis at a slight angle with the plane of the curve, the upper end of the axis being tilted outward and the lower, inward (Fig. 26). Both fangs on a side have the points twisted in the same direction.

Viewed under magnification, the fang material is sometimes transparent, sometimes translucent white, but often a mixture of the two, the transparent sections being flecked and striated with white. In the larger fangs, and in strong light, the pulp cavity can be seen as a shadow, terminating in a cone-shaped void within the fang point.

While the suture along the front of the fang is visible on the inner surface of the duct, as can be determined by examining fractured sections, it is less evident than on the exterior surface. It seems to be more of a shadow than an actual plane of separation, so perfect is the junction. Yet the experiments with immature fangs, in which the suture opens smoothly and evenly, show it to be a true joint.

#### The Fang Operating Mechanism

The bones of the rattlesnake head are illustrated and listed in Figs. 28-31. Of interest to those concerned with practical snake-bite problems is the highly specialized mechanism, whereby the fangs of these snakes can be tilted downward and forward, from an inactive position, folded against the roof of the mouth, to a striking or biting position, approximately perpendicular thereto. The fangs are so long that, were they permanently erect as in the elapine venomous snakes, they would entail a serious handicap, and, in fact, they would be so unwieldy that they could not be protected from breakage. This tilting mechanism is characteristic of the snakes of the families Viperidae and Crotalidae; although the bones involved differ considerably in shape amongst the several genera of these families, the arrangement, as a mechanical linkage, is consistently maintained. Of this the rattlers may serve as an illustrative example.

The fangs are carried, rigidly anchored, in the paired maxillaries, one on each side of the head. The maxillaries are shortened, as compared to those of snakes of other families, and are rotatable; it is this rotation that permits the tilting of the fangs. Considering the bones of the top of the head, that is, the frontal (3) and parietal (4, Fig. 29), as a datum, we find that some of the motion is secured by a slight hinge action of the prefrontal (2) at its attachment to the frontal; but most of it results from a combined sliding and hinge action where the maxillary (1) engages the prefrontal.

The bones whereby the tilting motion is transmitted to the maxillary are the quadrate (11), which drops downward posteriorly, thus causing the pterygoid (9) to advance; this in turn causes the forward motion of the ecto-

pterygoid or transpalatine (10), which, being connected to the maxillary below the hinge, pushes it forward. In Figs. 32 and 33 these bones are represented as a linkage, all the other bones of the skull, except those participating in the fang movement, being omitted for clarity. It should be understood that the anterior half of the pterygoid (9), where it is shown in parallel with the ectopterygoid (10) has little to do with the tilting mechanism, the ectopterygoid comprising much the stronger and more essential member of the linkage.

Posterior to the connection with the ectopterygoid, the pterygoid is strong and stiff, being heavily reinforced with wide flanges in a vertical plane. Anterior to this point it is relatively weak; the connection with the palatine (8) is not rigid, motion being permitted in all directions. At its anterior end the palatine is connected by one set of tendons to the inside face of the maxillary and, by another set, rather more loosely, to the prefrontal. The purpose of these attachments seems to be to limit the lateral movements of the forward end of the pterygoid; but all of the articulations are so loose that there is not much restriction, and there seems to be no effect of importance with respect to the rotation of the maxillary.

Returning to the ectopterygoid, at its point of connection to the pterygoid, we find this attachment to be rigid, with the effect of a splice, so that the ectopterygoid and the posterior half of the pterygoid act as a single member. The ectopterygoid is laterally compressed for stiffness. As it approaches the maxillary it twists into a horizontal plane, the upper edge outwardly, the inner edge in a contrary direction, so that when it reaches the maxillary the flange is horizontal. The front end is bow-shaped, and the outer ends of the bow form points of attachment to the sides of the maxillary, thus not only tilting it but tending to restrict its motion substantially to a vertical plane. The entire tilting mechanism is very positive in its action. The fangs on the two sides of the head are separately controlled, so that the snake may erect or retract either fang independently of the other. Thus he is enabled to use the fangs alternately in drawing in food, if the victim is relatively large or difficult to control. When a rattler is held for milking he will frequently raise one fang at a time and attempt to stab the venom cup or any other object within reach.

Consideration of the shape of the fang, taken in connection with the tilting mechanism, indicates, first, that it is better designed for use upon surfaces of relatively sharp curvature than against flat surfaces, i.e., upon smaller, rather than larger animals; and that the bite which follows the strike is of great importance, the fang being designed to take full advantage of this phase of the action. Although more attenuated in shape the fang is not unlike the talon of a hawk.

If, in the strike, a rattler's jaws are open so as to be exactly in opposition, that is, having an opening of 180 degrees, with the upper jaw held vertically, and if the fangs are erected perpendicularly so that the basal section points directly forward (Fig. 31), then the point section will be directed at an angle of about 25 degrees to any plane surface at which the blow be aimed, or 65 degrees from maxi-

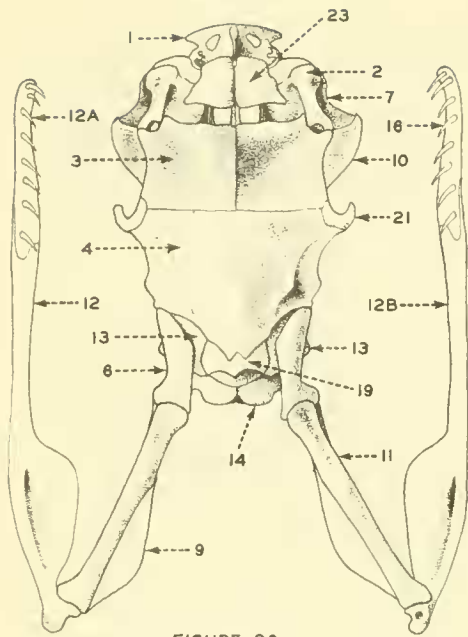


FIGURE 28  
DORSAL VIEW OF SKULL  
*C. RUBER*

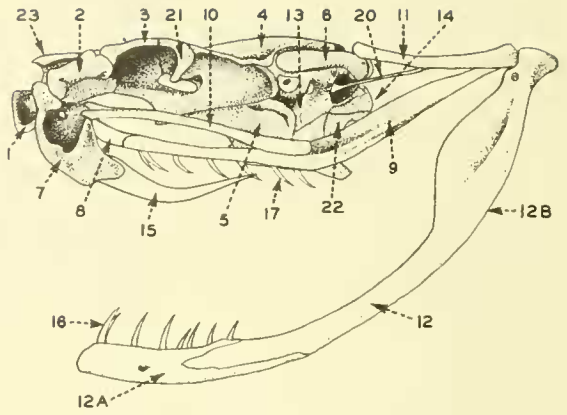


FIGURE 30  
LATERAL VIEW OF SKULL

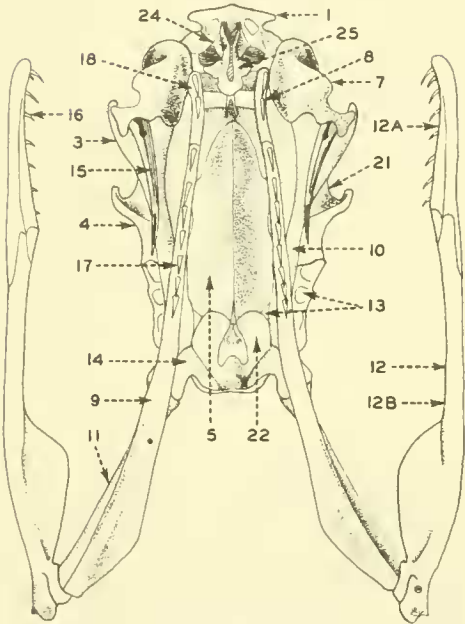


FIGURE 29  
VENTRAL VIEW OF SKULL

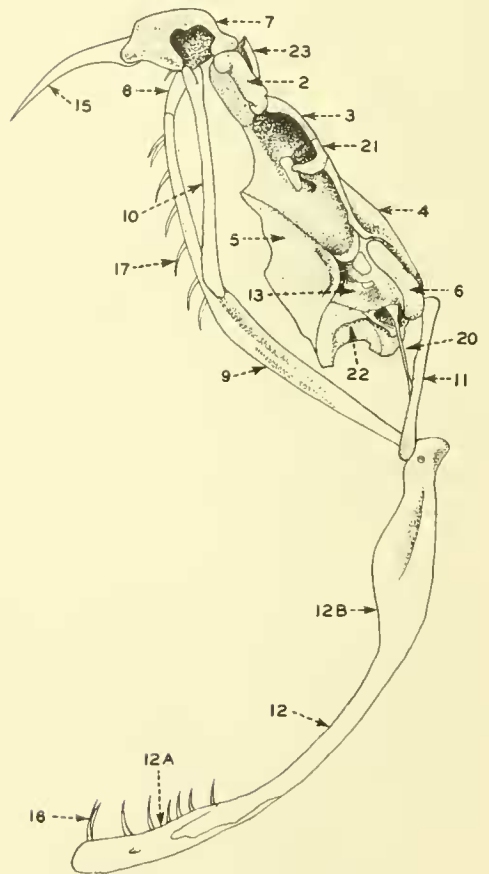


FIGURE 31  
LATERAL VIEW OF SKULL  
STRIKING POSTURE



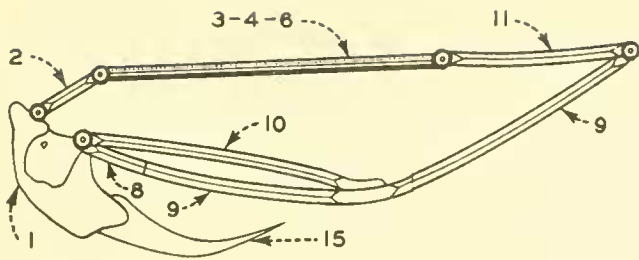


FIGURE 32  
FANG TILTING LINKAGE  
FANG FOLDED OUT OF USE

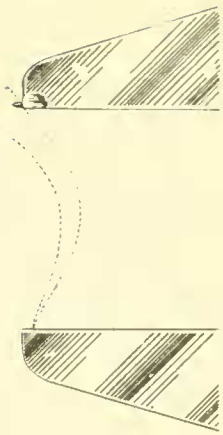


FIGURE 34  
METHOD OF  
MEASURING FANGS

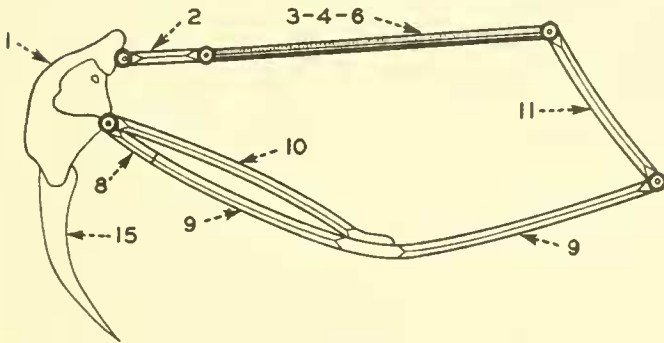


FIGURE 33  
FANG TILTING LINKAGE  
FANG ROTATED FORWARD FOR USE

Key to Figures 28 to 33  
The Bones of the Rattlesnake Skull

1. Premaxilla
2. Prefrontal (lachrymal of some authors)
3. Frontal
4. Parietal
5. Basisphenoid
6. Squamosal (supratemporal of some authors)
7. Maxilla (maxillary or supermaxillary)
8. Palatine (palatal)
9. Pterygoid (internal pterygoid)
10. Ectopterygoid (external pterygoid or transpalatine)
11. Quadrate
12. Mandible (mandibular)
  - 12A. Dentary
  - 12B. Articular
13. Pro-otic
14. Exoccipital (lateral occipital)
15. Poison fang
16. Mandibular teeth
17. Pterygoid teeth
18. Palatine teeth
19. Supraoccipital
20. Stapes (or columella auris)
21. Postfrontal
22. Basioccipital
23. Nasal
24. Turbinal
25. Vomer

mum effectiveness. Even allowing for a jaw opening greater than 180 degrees, and a tipping of the maxillary to permit the fangs to be erected more than 90 degrees (rattlesnakes can attain a greater angle, as may be observed by manipulating the venom cup in milking)\* there is still an oblique rather than a perpendicular approach of the point. But once the point has gained entrance, then both the curve in the fang and the folding action of the maxillary serve to accentuate the penetration produced by the squeezing pressure of the bite, particularly as the fang has a much smaller radius of curvature (about one-sixth) than the hinge distance of the upper jaw. It is true that the folding and the curve both sacrifice depth of penetration in favor of horizontal penetration, but they insure injection below the skin of the victim, which is the important point. This combined sliding with horizontal penetration is much less likely to be stopped by a bone than perpendicular penetration, and likewise the hook effect serves to hold to the prey or enemy momentarily. When the fang is folded, the emission aperture is directed inward toward the victim, which is a further advantage to the snake.

It is probable that at the end of the strike the snake's jaws are already tending to close, in which case the motion of the fang point, by reason of the combined head advance and jaw rotation, has a resultant motion more nearly in line with the fang-point axis. The fangs of those species having the least angle, such as durissus, molossus, and polystictus, are designed for more of a stabbing and less hooking action. The fangs of certain species of Bothrops are definitely of the stabbing type, as compared to the rattlers. This feature may possibly be correlated with venom quality; it is no doubt also of phylogenetic significance.

The folding is, of course, equally beneficial in providing a depository for the fang when not in use. When folded back against the upper jaw the base and the point are approximately level; the bulge of the curve fits into a groove in the lower jaw just outside of the mandibles.

#### Method of Fang Measurement

Before endeavoring to determine whether there are any differences worthy of note between the fangs of the several species of rattlesnakes, we must consider the variations to be found within a single species, so that we will not confuse mere individual differences with specific differences.

Our first study is made of fang length, followed by some considerations of fang shape, especially the nature of the central arc, and the angle between the two tangent sections.

The measurement of the length of a fang is found to be a rather involved procedure. First the protective sheath of tissue must be cleared away. The fang itself is of considerable fragility, especially in the smaller snakes. The active fang is imbedded in the maxillary socket, which hides the true base, so that its length over-all, either

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\* See also series of photographs in THE SUNDAY STAR, Washington, D.C., Gravure Section, p. 4, March 12, 1939.

along the curve, or in a straight line from base to point, cannot be determined without dissection. Nor can the junction, either with the edge of the socket or with the bony pedestal, be used as the proximal terminus, since this is irregular and cannot be located with accuracy. After some consideration of the problem, it was decided to use, as a criterion of length, the straight line distance from the lower end of the upper aperture, or lumen, to the point of the fang. This is, of course, merely a convenient arbitrary criterion; the actual length of the fang to the edge of the maxillary socket is greater and the full length, including the basic frustum, higher still. By fastening a needle to the side of a vernier caliper, so that the point protrudes about 1 mm. beyond the upper caliper jaw, and at the level of its measuring face, a convenient and practical measuring tool is provided. This point can be inserted in the upper lumen and then drawn downward until it engages the lower end of the slit; the lower jaw of the caliper is then brought up until it just contacts the tip of the fang and thus the length is determined (Fig. 34). Such a measurement can be made accurately to within 0.1 mm. Care must be taken not to bring up the jaw too firmly, as the extreme tip of the fang is very brittle and the point may be broken off without being noticed.

### Sexual Dimorphism

As is usual in problems of this character, before beginning studies of intraspecific variations, we must first give attention to individual variations (if an individual supplies more than one measurement or count) and to possible sexual dimorphism. In the present study four measurements may be made in each snake, for, as has been pointed out, almost every specimen has two functional and two fully developed reserve fangs.

We began our survey with the Platteville series of Crotalus viridis viridis, which is a large and homogeneous collection of specimens. In measurements made on 43 adult snakes of this series (measuring in each the functional and first reserve fangs), it was found that the average deviation in the fang length, from the mean of the several measurements in the same snake, was 1.14 per cent, with a standard deviation of 1.49 per cent. The maximum range between the longest and shortest fang (in any one snake), was found to be 0.5 mm., or 6.5 per cent, as this particular snake had fangs averaging 7.7 mm. The maximum variation of any fang from the mean of the four fangs in that specimen, was 4.8 per cent. These figures indicate a rather high degree of individual uniformity; that is, in any single snake, the two functional fangs and the first two reserves are almost exactly equal in size.

We next use the same series to determine whether sexual dimorphism is in evidence, or whether the measurements of the sexes may be combined in our subsequent studies.

It has already been shown (in Part V, of this series), that rattlers, with the exception of C. cerastes, have no sexual dimorphism in the ratio of head length to body length over-all. Thus, if the fang length is found to show no sexual dimorphism on a basis of head length, it will have none with respect to body length, and it is immaterial which we use as a datum in our study of the fangs.

One active fang per side--usually the right--was measured in 588 specimens of the Platteville series, 316 males and 272 females. The results were grouped by increments of 1 mm. in the head size. Taking the adults only, where sexual dimorphism would be evident if it exists at all, and considering only size-groups in which at least 9 individuals of each sex were available, to afford a fairly reliable sample, we have results which may be tabulated as follows:

Head size, mm.	Number of Specimens		Average Fang Length, mm.	
	Males	Females	Males	Females
26.0 - 26.9	9	14	5.23	5.28
27.0 - 27.9	17	15	5.44	5.50
28.0 - 28.9	34	39	5.57	5.71
29.0 - 29.9	25	26	5.82	5.81
30.0 - 30.9	19	24	5.97	5.92
31.0 - 31.9	26	23	6.21	6.35
32.0 - 32.9	23	29	6.49	6.55
33.0 - 33.9	28	31	6.74	6.56
34.0 - 34.9	27	14	6.97	6.72
35.0 - 35.9	16	9	7.04	7.10
36.0 - 36.9	17	11	7.16	7.01

It will be observed that the female fangs average larger in 6 size classes, and the males larger in 5; the algebraic sum of the differences is negligibly small. The variations evidently result from the fluctuations inherent in random sampling, rather than from a consistent sexual divergence.

In the same manner the San Lucan series of about 300 adult and adolescent specimens of Crotalus lucasensis was investigated. This material, collected by Capt. F. Lewis, was chosen because it is the most homogeneous series of large snakes of the cinereous group available to me. This group of diamond-back rattlesnakes is particularly important from the standpoint of snake-bite studies, as, in the United States, it is probable that more serious cases result from the bite of C. cinereous than all other rattlers combined. While I have available several hundred specimens of cinereous, they are from scattered localities throughout the wide range of the species; and, in the initial study of sexual dimorphism and fang growth-trends, it was desired to avoid the possible complications involved in combining snakes from areas in which they do not attain the same ultimate size (as is the case with cinereous in different parts of Arizona and Texas), since snakes of the same length might not represent the same age or point on the ontogenetic curve. The specimens of lucasensis, on the other hand, are from a single restricted area, and from their close relationship with cinereous it may be presumed that their growth-trends will be similar. Lucasensis is a decidedly larger snake than C. y. viridis, which permits a more accurate measurement of the fangs. The sexual comparisons in this species follow:

Head size, mm.	Number of Specimens		Average Fang Length, mm.	
	Males	Females	Males	Females
40.0 - 40.9	4	7	9.8	9.4
41.0 - 41.9	5	11	9.2	9.4
42.0 - 42.9	12	9	9.8	9.6
43.0 - 43.9	7	11	9.8	9.8
44.0 - 44.9	3	14	10.7	10.1
45.0 - 45.9	6	12	10.5	10.7
46.0 - 46.9	10	14	10.9	10.3
47.0 - 47.9	10	9	11.1	10.7

In this case a slight superiority of the males is indicated; however, it is of somewhat doubtful significance, owing to the relatively small numbers of specimens available in the several classes. Furthermore, it must be remembered that this series shows a considerable sexual dimorphism in body size (Part IV, p. 22); the result is that, in the higher groups in the above table, the females are decreasing in number and the males increasing. In a situation such as this the effect of grouping is to accentuate the differences between the means, which may account for the slight superiority of the males.

Thus it appears that sexual dimorphism is absent in one of these two species and is doubtfully evident in the other, and we proceed with our subsequent studies with the sexes combined. It will be remembered (Part V, p. 37) that C. cerastes is the only rattlesnake showing sexual dimorphism in the proportion of head length to body length over-all. This species may likewise prove to have sexual dimorphism in the fangs, either when correlated with the head size as a datum, or with body size; in fact it must inevitably show one or the other. However, the accurate determination of this point would require a larger series of adult cerastes from a single locality--say two or three hundred--than is now available to me.

#### Intraspecific Fang Correlations

In considering the length of a snake's fang we have the problem of comparing the size of one part of the body with another during ontogeny; in this case the length of the fang, either with the head length, or the body length over-all. Only infrequently do two body parts maintain a fixed ratio during growth, and the same absence of constant proportionality is true respecting the size of any single body part, or organ, in proportion to the body as a whole. This greatly complicates the size-relationship of any particular part, such as the fang. As a problem, the determination of fang proportionality is substantially the same as that of comparing the head length with the length of the body over-all, as developed in Part V of this series, which contained a discussion of the statistical methods involved. In the present instance we have the same problem of determining the character of a regression line and the nature of the dispersion about that line. For the method of attack the reader is directed to the former paper; the development will not be here repeated.

In this investigation, as in the head-length studies, we find it desirable to make an intensive survey of a few species, for the primary purpose of determining the nature of the variation as a scientific fact. This requires a considerable number of measurements to learn the type of regression line involved, and the nature and extent of the dispersion about that line. This is sufficient as far as intraspecific studies are concerned. If the relationship is found to be fundamentally complicated, that is, not expressible as a simple ratio, or even as a first degree equation, then we must determine to what extent our findings may be generalized or simplified for application to interspecific problems, without too great a sacrifice of accuracy. Such simplified expressions are essential, for the taxonomist has neither the time nor the material required for the determi-

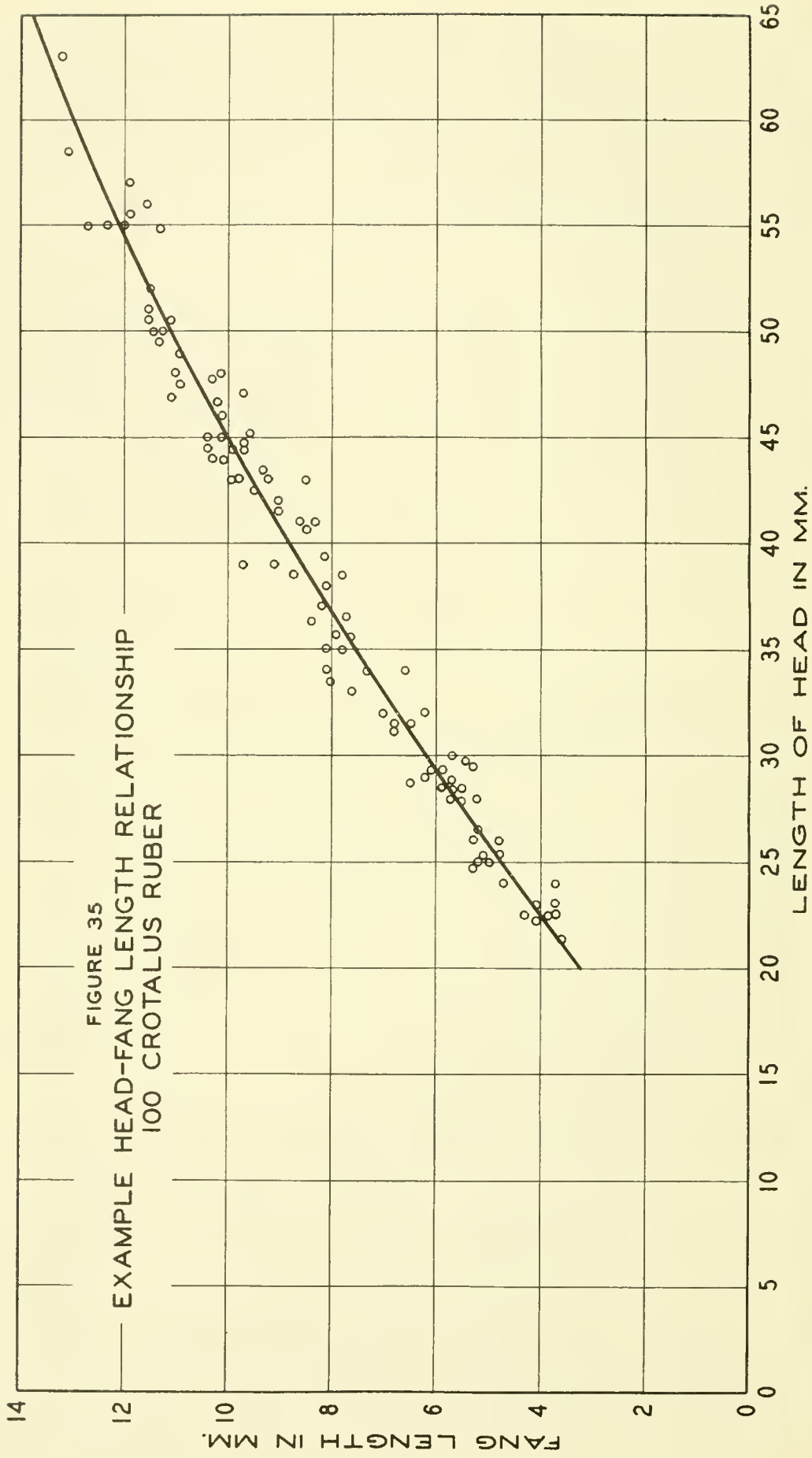


FIGURE 35  
 — EXAMPLE HEAD-FANG LENGTH RELATIONSHIP  
 100 CROTALUS RUBER

nation of the more involved formulas; hence, if the study is to have any practical value for interspecific comparisons, or indications of phylogeny, abridgment is necessary. As a matter of fact, it may well be stated at this point that it will seldom be found that the fangs will solve any taxonomic problem not more readily attacked by using other characteristics. However, when an entire genus is investigated certain trends are observable which add their weight to the phylogenetic indications derived from other characters.

This program has been carried out in the present study. A complete survey has been made of the variations in fang length in the Platteville series of C. v. viridis, and, to a somewhat lesser extent, in series of molossus, cinereous, lucasensis, and ruber. From the character of ontogenetical variation thus determined, simplified statements of relationship are evolved, which are sufficiently accurate for the practical purposes of species comparisons and the evaluation of differences. It is shown that there are interspecific differences in the ratios, both of the fang to head length, and to body length.

### Parabolic Regression Equations

For our first determination of the nature of the increase in fang length during ontogeny, we have taken a series of 100 specimens of C. ruber, equally distributed in age from birth to full adult growth. This species was selected as it is of rather large size and accurate measurements of the fangs are thereby facilitated. A homogeneous series from the vicinity of San Diego is available. Furthermore, we have at hand specimens taken at all seasons, especially during the spring, when the young of the year experience their most rapid growth. This is not the case in some of the largest available series, such as the Platteville series of C. v. viridis, wherein the concentration of juveniles taken at the season of hibernation necessitates certain special considerations, as mentioned hereafter.

Making one functional-fang measurement (F) in each of the 100 specimens of ruber, and plotting the results on rectangular co-ordinates, first against head length (H), and then body length over-all (L), we have the results as set forth graphically in Figs. 35 and 36.

Despite a considerable scatter, a slight curvature--an upward bulge in the center--is clearly shown in the trend of the points in both cases. For curves of this type, second degree parabolas of the form  $Y = fX^2 + gX + h$  will usually supply a satisfactory fit. Employing the usual method of curve fitting, we evolve the following equations, all quantities being expressed in millimeters:

$$F = - 0.00186H^2 + 0.393H - 3.940$$

and for the body length relationship

$$F = - 0.000002098L^2 + 0.013171L - 0.666$$

or, if the body length be expressed in meters, and the fang length in millimeters as before, we have the less awkward expression

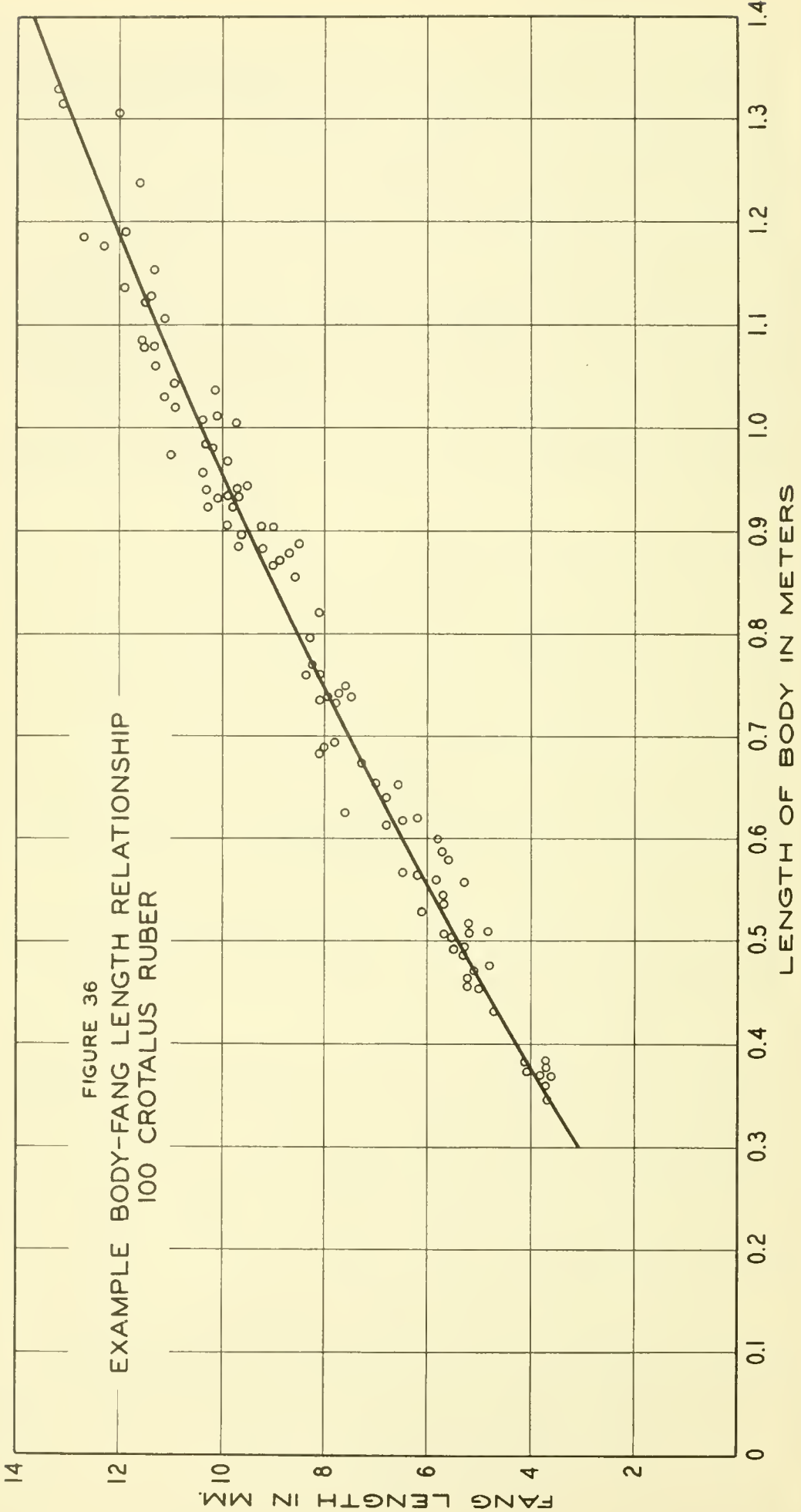


FIGURE 36  
 EXAMPLE BODY-FANG LENGTH RELATIONSHIP  
 100 CROTALUS RUBER



$$F = - 2.098L^2 + 13.171L - 0.666$$

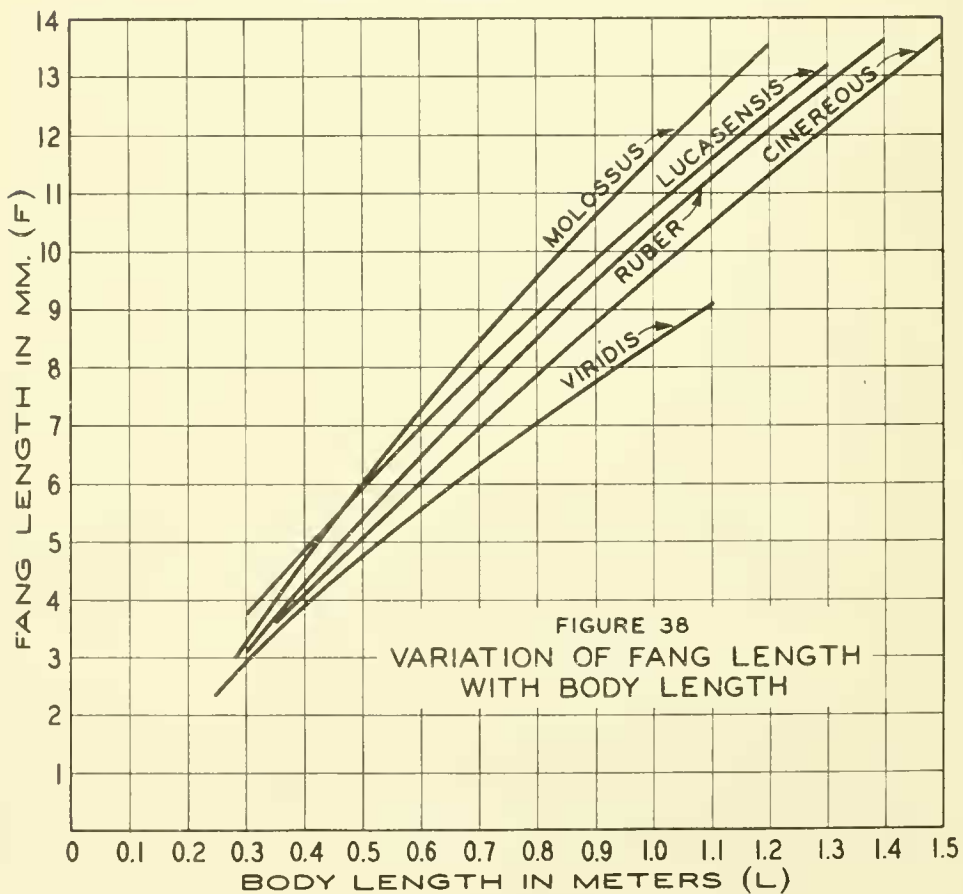
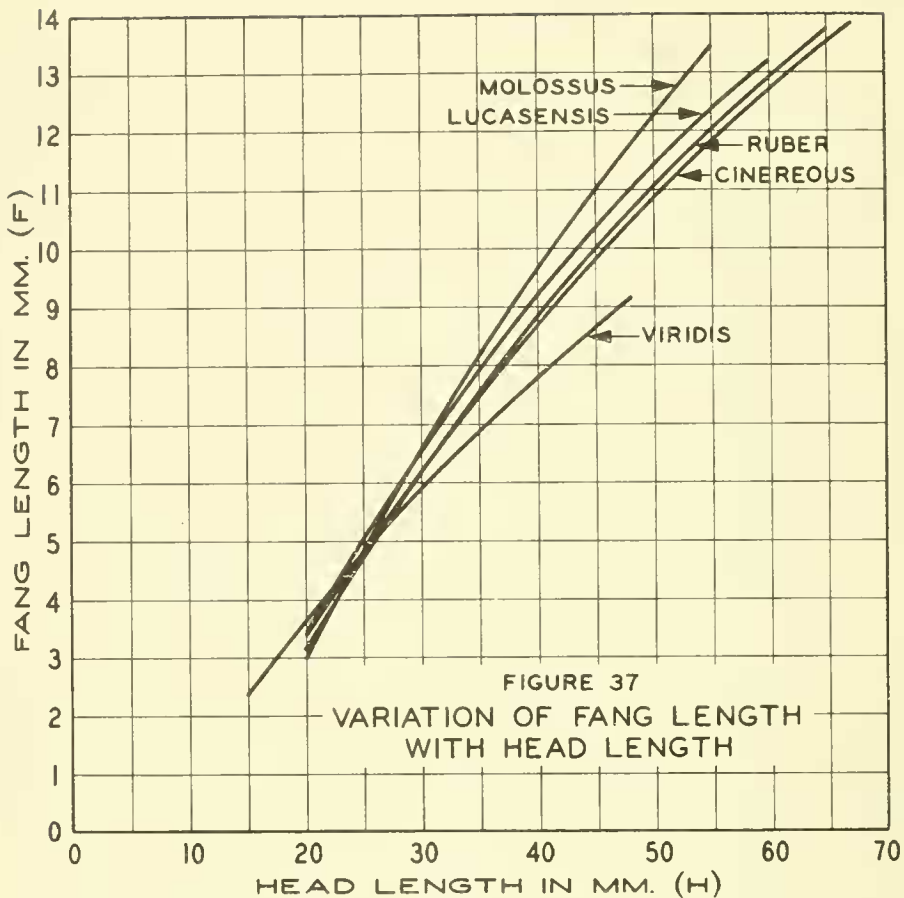
These curves are also shown in Figs. 35 and 36; they seem to afford a satisfactory fit of the averages of the points.

Before proceeding to the discussion of other forms of curves and other species, I wish to point out certain relationships which are evident from these curves by inspection. If tangents be drawn from the origin to each curve, we have at the point of tangency, a period of life at which the fang is growing\* at the same rate as the head, or body, as the case may be; that is to say, during this period the fang maintains a constant ratio with the head (or body). Earlier in life the growth of the fang is proportionately more rapid than that of the head; later it is slower. The same is true of the relationship with the body. But it must be understood that these constancies of ratio with the head, and with the body, do not occur at the same period of life. Also, as the curves are relatively flat, and the dispersion is considerable, we may, for practical purposes, assume the maintenance of a constant ratio for some distance on either side of the actual point of tangency. To illustrate, we find, from the F on H curve (Fig. 35), that, in the species ruber, the fangs maintain approximately a constant ratio with the head between head lengths of about 43 and 49 mm.<sup>♠</sup> Since we do not readily visualize the size of a rattler from its head length, we may translate these figures into body lengths by using  $H = 0.0374L + 8.4$ , as given in Table 19 of this series (Occ. Pap. No. 4, p. 38), and determine this substantially constant ratio to be maintained between body lengths of about 925 and 1085 mm. This is the young adult range. With respect to the F on L curve (Fig. 36), we find the point of tangency to be at about 560 mm., and a constant growth ratio to be continued from about 500 to 600 mm. This range represents rattlers of this species at an age of about 8 to 10 months. Hence it is seen that a constant ratio with body length over-all is reached early in life, followed by a proportionately slower growth of the fang than the body. Later the snake enters a period during which the fang is growing at the same rate as the head, after which it lags slightly behind the head in proportionate growth. All of these conclusions are inherent in the three equations relating to F, H, and L, but it is desired to point them out devoid of mathematical terminology. The same types of relationships are found to be true of other species, except that in some cases the constant term  $h$ , in the equation  $F = fL^2 + gL + h$ , is positive. Where this is true, the proportional growth-rate of the fang

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\* The word "growing" does not, of course, mean that an individual fang grows, after it has become the functional fang. Growth as here used, connotes the procession of sizes which the succession of functional fangs attain during the period under discussion. Growth is actually by a series of small steps.

♠ The point of tangency may usually be located with sufficient accuracy by eye; analytically it may be found at  $X = \sqrt{h/f}$  where  $f$  and  $h$  are the coefficients in the regression equation  $F = fH^2 + gH + h$ , or  $F = fL^2 + gL + h$ , as the case may be. If  $f$  and  $h$  are of unlike signs, then there is no real point of tangency, that is, no condition of constant proportionality.



is always less than that of the body, even in the juvenile stage.

The second degree parabolic equations covering several other species, from birth to adulthood, were determined to be as follows, the ruber equations being repeated for comparative purposes. In the F-L equations, L is in meters to simplify the expressions.

<u>Species</u>	<u>No. of Specimens</u>	<u>F in Terms of H</u>
<u>C. m. molossus</u>	44	- 0.00246H <sup>2</sup> + 0.483H - 5.680
<u>C. cinereous</u>	52	- 0.00157H <sup>2</sup> + 0.358H - 3.120
<u>C. lucasensis</u>	270	- 0.00225H <sup>2</sup> + 0.424H - 4.180
<u>C. ruber</u>	100	- 0.00186H <sup>2</sup> + 0.393H - 3.940
<u>C. v. viridis</u> (Platteville)	588	- 0.00193H <sup>2</sup> + 0.325H - 2.100

<u>Species</u>	<u>No. of Specimens</u>	<u>F in Terms of L</u> (L expressed in meters)
<u>C. m. molossus</u>	44	- 3.036L <sup>2</sup> + 15.942L - 1.224
<u>C. cinereous</u>	52	- 0.625L <sup>2</sup> + 9.885L + 0.298
<u>C. lucasensis</u>	270	- 1.922L <sup>2</sup> + 12.514L + 0.158
<u>C. ruber</u>	100	- 2.098L <sup>2</sup> + 13.171L - 0.666
<u>C. v. viridis</u> (Platteville)	594	- 2.009L <sup>2</sup> + 10.414L + 0.039

These curves are shown in Figs. 37 and 38. A general similarity in the curves is apparent, although each species shows some individuality, as is likewise indicated by the constants of the equations. With respect to these last, it should be made clear that the original data do not justify the number of significant figures here given. However, they have been retained for the purpose of checking the quantitative errors introduced by the various approximations subsequently to be discussed.

Of course, there is no reason, inherent in the relationship between fang and head, or fang and body, why a second degree parabola should be followed. It is merely found that this curve supplies a fit, with close enough adherence, to give a solution satisfactory for our purposes, especially having in mind the dispersion of the points, which in part results from individual differences, and partly from the errors inherent in laboratory measurements of such irregular objects as the heads and fangs of rattlesnakes.

It will be worth while to investigate two other types of curves, simple parabolas of the form  $Y = dX^k$ , and exponential curves of the type  $Y = mm^x$ . The first produces a straight line on log-log, and the second on semi-log cross-section paper. The use of semi-log co-ordinates is found to produce no results of interest. On log-log co-ordinates we find, in the special case of the large Platteville series, a close approach to a straight line relationship for the juveniles and for the adults; but the two straight lines are not consistent with each other--that is, they do not intersect in the adolescent range, as would be evident if there were a

transition in the growth gradient as found by Huxley in certain similar proportionality problems.\* In the other cases, log-log co-ordinates result in rather flat, but still quite apparent, curves. Thus, parabolas of the form  $Y = dX^k$  do not result in a complete and logical solution. However, they are worth while to determine, since they give a moderately close fit, especially within any limited life-range (adults only, for example), and they are useful in the manipulation of ratios.

The failure of the young of the year, in the Platteville series, to follow a regression line consistent with that of the adolescents and adults, no doubt results from the same conditions which produced a nonconformity in the correlation of body weight with length over-all, as discussed in a prior section of these studies (Occ. Pap. No. 3, p. 50). In that case it was pointed out that this series, representing young of the year at the hibernating season only, comprises what might be called a dispersion, rather than a growth group. For this reason we do not consider that the series gives a true picture of the interrelation between juvenile and adult regression lines.

In the case of the ruber series, it is possible, without too great a stretch of the imagination, to draw two intersecting straight lines, on log-log co-ordinates, one of which represents the juveniles, and the other the adults, with a satisfactory degree of accuracy--more satisfactory than both together can be represented by a single straight line. But it is important to note that the division between the two must be selected in a purely arbitrary manner; no natural point of flexure is evident. This is contrary to what Huxley has found (loc. cit. p. 10) in certain similar situations, where he has shown a sudden change in the growth gradient. In such a case two consecutive straight lines on log-log paper, with a short flexure between, is indicated as the most appropriate graphical representation.

It has been stated that, although curves of the form  $Y = dX^k$  do not exactly fit the growth trend of the fangs throughout the entire ontogenetical range, we can secure an entirely satisfactory fit by restricting consideration to a part of the life span. As the adults of any species are of the most importance, insofar as the practical considerations of the snake-bite problem are concerned, we are justified in concentrating our investigations on the adult range. We find the following equations to supply satisfactory fits within this range:

<u>Species</u>	<u>Constants in <math>F = d_1 H^{k_1}</math></u>		<u>Constants in <math>F = d_2 L^{k_2}</math></u>	
	$d_1$	$k_1$	$d_2$	$k_2$
<u>C.m.molossus</u>	0.165	1.096	0.0235	0.896
<u>C.cinereous</u>	0.201	1.014	0.0192	0.899
<u>C.lucasensis</u>	0.251	0.970	0.0351	0.828
<u>C.ruber</u>	0.177	1.052	0.0207	0.899
<u>C.v.viridis</u>	0.209	0.984	0.0355	0.791
(Platteville)				

\* Julian Huxley, Problems of Relative Growth; New York, 1932, p. 10.

Exponents of the type of  $k$  in the above equations are referred to by Huxley (loc. cit. p. 8) as "constant differential growth ratios". Where  $L$  is the independent variable,  $k$  becomes the "growth-coefficient" of the fang.

From these last equations there may be readily derived body-proportionality equations showing the number of times the fang length is contained in the head or body length. We have the following results:

<u>Species</u>	<u>Constants in <math>H/F = d_3 H^{k_3}</math></u>		<u>Constants in <math>L/F = d_4 L^{k_4}</math></u>	
	$d_3$	$k_3$	$d_4$	$k_4$
<u>C.m.molossus</u>	6.06	-0.096	42.55	0.104
<u>C.cinereous</u>	4.98	-0.014	52.08	0.101
<u>C.lucasensis</u>	3.98	0.030	28.49	0.172
<u>C.ruber</u>	5.65	-0.052	48.31	0.101
<u>C.v.viridis</u> (Platteville)	4.79	0.016	28.17	0.209

If these equations do nothing more, they show again that the fang length does not bear a constant ratio, either to the body or to the head length, through the adult stage, since this would follow only if  $k_3$  and  $k_4$  were zero. The fact that in the  $H/F$  relationship,  $k_3$  approximates zero, and varies from plus to minus in the different species, indicates that the ratio  $H/F$  is approximately constant within the adult range.

Before proceeding with the dispersion studies, I wish to comment on three aspects of the results thus far obtained. First, it is to be remembered that our criterion of fang length (i.e. the distance from upper lumen to tip) is more or less artificial. The over-all length of the fang, along the curve, is not proportional to this straight line distance during ontogeny, because the angle subtending the arc of the central curve changes during life, as will be subsequently discussed. Hence, the actual length of the fang, as measured along the bend, might follow a different regression equation, when correlated with head or body length, than the distance which I have arbitrarily called the fang length,  $F$ . For example, in a series of adamanteus fangs having an  $F$  length of 14 to 17 mm., the distance along the curve was found to be from 10.5 to 13.8 per cent greater than  $F$ , the average being 12.8 per cent. In addition, the distance from the lower edge of the upper lumen to the distal edge of the maxillary socket was from 3 to 4 mm. (see dimension E, Table 30). But  $F$  does have the advantage of being measurable with considerable accuracy; also, the distance is probably of more practical importance in a consideration of snake bite than the length of the fang along the curve. I merely call attention to this arbitrary character of  $F$  as a possible explanation of the rather involved formulas which correlate  $F$  with  $H$  and with  $L$ .

Secondly, I have not canvassed all the types of equations, even of the second degree, which might have proved to fit closely the actual facts in these examples. Having determined that constants for curves of the forms  $Y = fX^2 + gX + h$ , for complete ontogeny, and  $Y = dX^k$  for the adult range, could be found which would produce satisfactory fits, especially having in mind the scatter of individual

TABLE 22

CORRELATION OF FANG AND HEAD LENGTH: PLATTEVILLE SERIES OF *C. v. viridis*

		Fang Length in Millimeters												Total	
		2.0 to 2.4	2.5 to 2.9	3.0 to 3.4	3.5 to 3.9	4.0 to 4.4	4.5 to 4.9	5.0 to 5.4	5.5 to 5.9	6.0 to 6.4	6.5 to 6.9	7.0 to 7.4	7.5 to 7.9		8.0 to 8.4
Head Length in Millimeters	15.0-15.9		1											1	
	16.0-16.9	2	12											16	
	17.0-17.9		12	2										22	
	18.0-18.9		9	14	1									18	
	19.0-19.9		1	9	2									12	
	20.0-20.9														
	21.0-21.9														
	22.0-22.9														
	23.0-23.9														
	24.0-24.9						2	1						3	
	25.0-25.9						3	3						6	
	26.0-26.9						6	7						23	
	27.0-27.9					1	16	13	2					32	
	28.0-28.9						21	39	12					73	
	29.0-29.9						9	26	14	1	1			51	
	30.0-30.9						3	14	24	2				43	
	31.0-31.9						1	7	28	12	1			49	
	32.0-32.9							5	15	25	6	1		52	
	33.0-33.9								22	24	13			59	
	34.0-34.9								6	16	17	2		41	
	35.0-35.9									12	9	2	1	24	
36.0-36.9									1	5	19	2	27		
37.0-37.9										1	8	6	16		
38.0-38.9											4	5	10		
39.0-39.9												2	2		
40.0-40.9										1	2	3	6		
41.0-41.9											1	1	2		
Total		2	29	35	3		12	61	114	124	99	79	21	9	588

TABLE 23

CORRELATION OF FANG AND BODY LENGTH: PLATTEVILLE SERIES OF *C. v. viridis*

		Fang Length in Millimeters												Total	
		2.0 to 2.4	2.5 to 2.9	3.0 to 3.4	3.5 to 3.9	4.0 to 4.4	4.5 to 4.9	5.0 to 5.4	5.5 to 5.9	6.0 to 6.4	6.5 to 6.9	7.0 to 7.4	7.5 to 7.9		8.0 to 8.4
Body Length in Millimeters	220-249		1											1	
	250-279	1	6	2										9	
	280-309	11	13	8										22	
	310-339		8	19	1									28	
	340-369			6	1									7	
	370-399				1									1	
	400-429														
	430-459														
	460-489						1							1	
	490-519						4	1						5	
	520-549						3	8	6					17	
	550-579						4	18	11	1				34	
	580-609							24	27	4				55	
	610-639							7	30	22				59	
	640-669							3	30	20				57	
	670-699								8	24	6	2		40	
	700-729								4	26	24	3		57	
	730-759								2	17	26	13	1	59	
	760-789									10	25	19	3	57	
	790-819									2	10	18	2	32	
	820-849										3	14	5	22	
850-879										2	6	5	3	16	
880-909											3	3	3	9	
910-939											1	2	3	6	
Total		2	28	35	3		12	61	118	126	99	80	21	9	594

points, I have deemed it unnecessary to look further. (See pp. 44 & 47). Other types of curves giving close fits could no doubt be derived, but they would be no easier to use, nor more intelligible than these; and there would be no essential theoretical reason for their adoption in the place of those here proposed. In fact, if any curve is to be justified on theoretical grounds, it is probably  $Y = dX^k$  (Huxley, loc. cit., p. 30).

Thirdly, I realize that these curves are only interesting as showing the facts of body proportionalities; they are not in such form as to be of much service to the taxonomist. An equivalent amount of detail with respect to all species would be fruitless. If the fang size is to be of any practical interest, its relationship with the head and body sizes must be expressed in simpler form, even though some errors be introduced thereby. For this reason it appears advisable to make some determinations of the straight lines of best fit; then we may note the extent of the error introduced by this simplification. We must also find how nearly constant H/F and L/F are, within limited length-ranges, to see whether practical use can be made of these easily determined ratios in comparing species.

### Straight Line Regressions in the Adult Range

It will be observed that the coefficients of the  $X^2$  terms of the parabolic equations are small, which means that the curves are relatively flat. This is verified by an inspection of the curves themselves, Figs. 37 and 38. If we are willing to restrict the applicability of our straight lines to limited ontogenetical periods, the adult range for example, the errors introduced by using them, in the place of curves of higher degree, will not be important. As far as problems involving fang length may have any practical value, consideration of adults is certainly most important, since the adults are most dangerous. Similarly, from the taxonomic or phylogenetic standpoint, the adults are of greater interest, for species differences may be more accurately determined in the adult state, and are more impressive than differences between juveniles.

Tables 22 and 23 are correlation tables of the Platteville series of viridis on a basis of head length and body length over-all, respectively. From these the straight lines of best fit were found to be as follows:

#### Viridis (Platteville)

All ages	$F = 0.223H - 0.81$
	and $F = 8.22L + 0.55$
Adults and adolescents only	$F = 0.195H + 0.09$
	and $F = 7.12L + 1.33$

To simplify the F on L expressions, L is given in meters; all other quantities are in millimeters. The equation presumed to represent all ages is not to be considered accurate, since the range is too wide to permit a straight line to supply a satisfactory fit.

By similar methods the straight lines of best fit were determined for the four other species which we have in-

TABLE 24

COMPARISONS OF CALCULATED VALUES OF F  
USING DIFFERENT TYPES OF EQUATIONS

ADULT RANGE ONLY

	Second Degree Parabola ( $Y = fX^2 + gX + h$ )	Simple Parabola ( $Y = dX^k$ )	Straight Line ( $Y = aX + b$ )
<u>Viridis</u>			
L			
500	4.74	4.84	4.89
600	5.56	5.60	5.60
700	6.34	6.32	6.31
800	7.04	7.03	7.02
900	7.78	7.71	7.74
1000	8.44	8.38	8.45
H			
25	4.82	4.96	4.97
30	5.92	5.94	5.94
35	6.92	6.91	6.92
40	7.82	7.88	7.89
45	8.63	8.84	8.87
<u>Lucasensis</u>			
L			
500	5.93	6.03	6.16
600	6.97	7.01	7.05
700	7.98	7.96	7.95
800	8.94	8.89	8.84
900	9.86	9.80	9.74
1000	10.75	10.70	10.63
1100	11.60	11.58	11.52
1200	12.41	12.45	12.42
1300	13.18	13.29	13.32
H			
35	7.92	7.90	7.91
40	9.20	8.99	9.08
45	10.37	10.08	10.25
50	11.42	11.16	11.42
55	12.36	12.25	12.59
60	13.19	13.32	13.76



vestigated, using only adults and adolescents exceeding 500 mm. in body length. The results follow:

<u>Molossus</u>	F = 0.261H - 0.82	F = 10.50L + 1.12
<u>Cinereous</u>	F = 0.217H - 0.11	F = 8.61L + 0.89
<u>Lucasensis</u>	F = 0.234H - 0.28	F = 8.95L + 1.68
<u>Ruber</u>	F = 0.228H - 0.41	F = 9.10L + 1.17

It would have been sufficiently accurate to obtain these straight lines graphically by paralleling, as nearly as possible, the points on the parabolas representing the adults. However, this calculation gives a check on the previous computations.

It is quite apparent that, if we assume the second degree parabola to be the true curve of best fit, we can determine either straight lines, or simple parabolas (as we may desire), which will pass through any two points on the original curves. The closer the points are together--that is, the shorter the life range between them--the closer will the new approximating curves adhere to the original second degree parabola.

We are now in a position to compare these results with the parabolic equations previously discussed, to learn the extent of the errors introduced by the use of the simplified straight line formulas. For reasons already mentioned, we restrict our comparisons to the adolescent-adult range. The results are shown in Table 24 for the species lucasensis and viridis.

This table indicates that the differences resulting from the use of these three types of equations are relatively small--small indeed, compared with the fluctuations between specimens. It will be observed that the results calculated by the approximate equations supply figures usually not deviating from those secured from the second degree parabolas by more than 0.1 mm. Thus, consideration of the parabolic equations is justified only as a matter of theoretical interest; the differences are not of sufficient magnitude to warrant their retention in most studies, for to continue their use introduces a refinement hardly justified by the accuracy of measurements involved in the original laboratory data. However, we must be careful to apply the straight line equations only to the limited length-ranges upon which they are based, and for which they are designed. If we were to use these approximate equations for the computation of juvenile fang lengths, important errors would be introduced, as shown by the following examples: At a body length of 300 mm. a juvenile ruber has a fang length of 3.1 mm.; the straight line equation gives a result of 3.9 mm., an error of 26 per cent. Similarly, a juvenile cinereous having a head length of 20 mm. will have a fang length of about 3.4 mm. The use of the straight line formula gives a result of 4.2 mm., an error of 24 per cent. It is seen that these equations are useless when applied to periods of life for which they are inappropriate.

It is quite feasible to derive multiple regression equations of the first or higher degrees to fit the correlations of F, H, and L, but the dispersions are too great to permit such equations (with respect to the relative sizes of the coefficients) to have much value for interspecific comparisons. As an example, the first degree multiple regres-

sion equation for 44 specimens of C. cinereous over 500 mm. in length was found to be:

$$F = 0.00391L + 0.1033H + 0.770$$

While discussing the matter of straight line regressions, it may be noted that, if we determine from the H on L relationship developed in Part V, and the F on H equation presented above, a relationship between F and L, the result may be used as a check with the new F on L relationship developed. We have the following results:

	<u>Determination Through H</u>	<u>Direct Determination</u>
<u>C.v.viridis</u> (Platteville)	$F = 6.93L + 1.45$	$F = 7.12L + 1.33$
<u>C.lucasensis</u>	$F = 8.78L + 2.20$	$F = 8.95L + 1.68$

The discrepancies noted result from the lack of applicability of the straight line formulas to the F-L relationship, and in part to the least-squares theory involved in their derivation.

### Dispersion

Coming now to the dispersion, or the scatter of individual fang measurements about the regression lines which represent the average conditions of a species, I think it worth while to investigate two phases: the extent of the dispersion, and whether it remains constant during life on a proportionality basis. For this purpose I have investigated the Platteville series of C. v. viridis during the adolescent-adult stage; the juveniles have been omitted for reasons previously mentioned. Using the equations  $F = 0.209H^{0.984}$ , and  $F = 0.0355L^{0.791}$ , I have determined the deviation of the fang length of each specimen from the standard or normal fang length given by the equation. These deviations were tabulated as percentages of their respective normal values; the resulting percentages were then gathered into arrays, and their standard deviations calculated.\* In a previous section of this study (Occ. Pap. No. 4, p. 11), I have explained my preference for this method of calculation, as an indication of the character of the dispersion surface, in the place of the usual standard error of estimate. In the present instance we reach the following conclusions with respect to the Platteville series of viridis:

Coefficient of variation, F on H, 5.67 per cent;

and of F on L, 5.23 per cent.

Further analyzing the adolescents and small adults as one group, and comparing them with the largest adult specimens, as a second group, we find an indication of reduced dispersion in the largest sizes. The results follow, the figures indicating the coefficients of variation:

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\* See Occ. Pap. No. 4, pp. 13 and 22, for a more complete discussion of the method.

	<u>Adolescents</u> <u>or Young Adults</u>	<u>Large Adults</u>
Basis, head length	5.90	5.01
Basis, body length	5.19	5.03

A reduction of dispersion is evident; however, analysis shows the differences to lack significance, although approaching this level in the first case, where the difference, divided by its standard error, reaches 1.55.

In comparisons of the dispersions of body parts or scale counts, taken from juveniles and adults respectively, we are checking a matter of considerable intrinsic interest: What is the trend of the dispersion of any character during ontogeny--are juveniles or adults more consistent and uniform? There are two conflicting tendencies, or forces, and it is desirable to determine which has the superior effect. First, there is the tendency to suppress aberrant juveniles, through the unsuitability, or even the definitely lethal qualities, involved in their deviations from the species mode, thus tending to decrease dispersion as a population ages. Secondly, there are the environmental effects on the individual during growth, through such conditions as the availability of food, the results of accident or disease, favorable or unfavorable habitats, or other matters affecting any individual as compared to the fellow members of his group. Thus this diversity of conditions would increase dispersion in the adult population encountering it. In summary, juvenile dispersion should be high because of natal aberrance; adult dispersion should be high because of the hazards of life.

Particularly interesting in studies of this kind are those characters which change during growth, as, for example, the width of the proximal rattle, or head length as a function of body length. On the other hand, scale count dispersions, such as the number of ventrals, which do not change during ontogeny, should show only the effect of the suppression of aberrant juveniles. A statistical calculation demonstrating a significant difference in the dispersion of any character amongst the juveniles, as compared to the adults, is of utility in determining which of these conflicting effects seems to have the superior influence.

I have already shown (Occ. Pap. No. 4, p. 17) that the dispersion in the head length, compared with body length over-all, tends to increase with age. The opposite effect is indicated here, with respect to the fangs, but the differences lack significance. Again, this cannot be considered particularly important, because the true juveniles have been eliminated--our comparison is only between adolescents and small adults on the one hand and large adults on the other.

The similarity of the dispersions of the adolescents and the large adults, when computed on a percentage basis, demonstrates the validity of the logical supposition that deviations of any individual from a mode do not remain constant on an absolute-measurement basis as the individual grows. On the contrary it remains constant on a basis of proportionality; that is, a young rattler having a fang 5 per cent greater than the average of his fellows will continue to deviate, as he grows, by about 5 per cent, rather than maintaining a constant difference in millimeters. Were the latter the case,

the dispersion would decrease markedly as the snakes age, a condition apparent neither here nor in the studies of head length (Occ. Pap. No. 4, p. 11).

Thus far I have shown that the dispersion about the regression line, whether on a basis of head or body length, remains constant with a coefficient of variation of about 5.5 per cent of the mean fang length at that age. A cross section of the dispersion surface is substantially normal. This figure of 5.5 per cent means that the consistency of rattle-snake fang measurements may be described thus: Half of all the fangs measured will come within 4 per cent of the mean fang length at any body size; less than 7 per cent of those measured will deviate more than 10 per cent above or below this mean. For example, take the species lucasensis. A group of specimens 925 mm. long will have fangs averaging 10 mm. long. Over half the specimens will have fangs between 9.6 and 10.4 mm.; and fewer than 7 per cent of the fangs will be less than 9 or more than 11 mm. This indicates a character consistent enough, within a species, to warrant the making of comparisons between species.

As a matter of interest with respect to methods of computation, the following statistics resulting from the correlations contained in Tables 22 and 23 are presented. It must be remembered that the standard error of estimate thus calculated, visualizes the deviations from the regression line as being constant in amount, rather than in percentage during ontogeny; and likewise the deviations are measured from the straight line of best fit rather than from a parabola.

F on H      F on L

Platteville viridis

Adults and juveniles

Coefficient of correlation, <u>r</u>	0.961	0.982
Standard error of estimate, mm.	0.353	0.239
Standard error of estimate, % of mean	5.93	4.04

Adults only

Coefficient of correlation, <u>r</u>	0.887	0.985
Standard error of estimate, mm.	0.344	0.332
Standard error of estimate, % of mean	5.48	5.29

Similar statistics of three other species which have been fully investigated are as follows, adult ranges only being considered:

Cinereous   Lucasensis   Ruber

F on H

Coefficient of correlation, <u>r</u>	0.944	0.903	0.893
Standard error of estimate, mm.	0.659	0.650	0.899
Standard error of estimate, % of mean	7.29	6.20	9.96

F on L

Coefficient of correlation, <u>r</u>	0.967	0.924	0.919
Standard error of estimate, mm.	0.503	0.588	0.788
Standard error of estimate, % of mean	5.61	5.64	8.73

It will be observed that the standard error of estimate, as a percentage of the mean fang length, is, in the case of the Platteville adults, in fair agreement with the coefficient of variation determined by the other method.

#### Choice of a Basis of Comparison for Interspecific Studies

It will be noted from these statistics that the coefficient of correlation  $r$  is higher, when calculated between fang length and length over-all, than when the fang is correlated with head length. However, I do not consider the fang to body-length correlation as necessarily the most important, or useful, despite this result. First it may be attributed, at least in part, to the fact that body lengths can be measured more accurately than head lengths. Under such circumstances, if perfect correlation were a fact of nature, our laboratory results would indicate a higher value of  $r$  in the correlation of F on L, than in F on H. Secondly, it must be remembered that, even though the points may adhere closer to the F on L regression line, than to that of F on H, this does not mean that the fang, during ontogeny, maintains a more nearly constant ratio with L than it does with H. We have already shown that in early life L/F is more nearly constant, while, in the more important adult stage, H/F tends to become constant.

A high coefficient of correlation means only close adherence to the regression line, which may well be a matter of accuracy in measurement as above suggested; the constancy of the ratio, however, depends on the direction of the line, which is a more important criterion in this case. After all, it must be remembered that the fang is a part of the head and a closer relationship should be expected, in both intraspecies and interspecies comparisons, between F and H than between F and L. So while we find a closer correlation, as shown by individual variations, between F and L than F and H; we find a closer relationship, as an ontogenetical proportion, between F and H than between F and L, which is increasingly manifest in later life. To illustrate this, we take the Platteville series of C. v. viridis, and the parabolic regression lines already found. Assume a snake with a fang length of 5 mm. We find that he will have a head length of 25.7 mm. and a body length over-all of 530 mm. Now let this snake grow until he has a fang length of 10 mm. His head length becomes 55.5 mm., and his body length 1270 mm. So while his fang increases 100 per cent, his head increases 120 per cent, but his body length increases by 140 per cent. Similarly in lucasensis, an increase of fang length from 6 to 12 mm. involves an increase in head length of 90 per cent, in contrast to a body length increase of 125 per cent. Thus we see that the fang grows more nearly in proportion to head growth than to body growth. Of course, the same relationship will be demonstrated if we let L or H double and determine what happens to the other two variables. For example, in the Platteville series, if the body increases from 500 to 1000 mm., or 100 per cent, the head length increases 75 per cent and the fang length 78 per cent, thus showing the closer agreement in proportionality between F and H than between F and L.

This is to a certain extent a repetition of the interrelations initially set forth with respect to C. ruber (p. 27), where it was shown that juvenile fangs increase in

TABLE 25

COMPARISON OF FANG LENGTHS BETWEEN SPECIES  
ON A BASIS OF HEAD LENGTH

Head Length in mm.	Fang Length in mm.				
	Molossus	Cinereous	Lucasensis	Ruber	Viridis
20	2.99	3.40	3.41	3.17	3.63
25	4.85	4.84	5.03	4.71	4.82
30	6.58	6.20	6.53	6.17	5.92
35	8.19	7.47	7.92	7.52	6.92
40	9.68	8.67	9.20	8.79	7.82
45	11.05	9.79	10.37	9.96	8.63
50	12.29	10.84	11.42	11.05	9.34
55	13.41	11.80	12.36	12.03	9.95
60	14.41	12.69	13.19	12.93	10.47
65	15.28	13.49	13.91	13.73	10.89
70	16.03	14.22	14.51	14.44	11.22

TABLE 26

COMPARISON OF FANG LENGTHS BETWEEN SPECIES  
ON A BASIS OF BODY LENGTH

Body Length in mm.	Fang Length in mm.				
	Molossus	Cinereous	Lucasensis	Ruber	Viridis
300	3.29	3.20	3.74	3.10	2.98
400	4.67	4.15	4.86	4.27	3.88
500	5.99	5.08	5.93	5.39	4.74
600	7.25	6.00	6.97	6.48	5.56
700	8.45	6.91	7.98	7.53	6.34
800	9.59	7.81	8.94	8.53	7.08
900	10.66	8.67	9.86	9.49	7.78
1000	11.68	9.56	10.75	10.41	8.44
1100	12.64	10.41	11.60	11.28	9.06
1200	13.53	11.26	12.41	12.12	9.64
1300	14.37	12.09	13.18	12.91	10.18
1400	15.14	12.91	13.91	13.66	10.68

TABLE 27

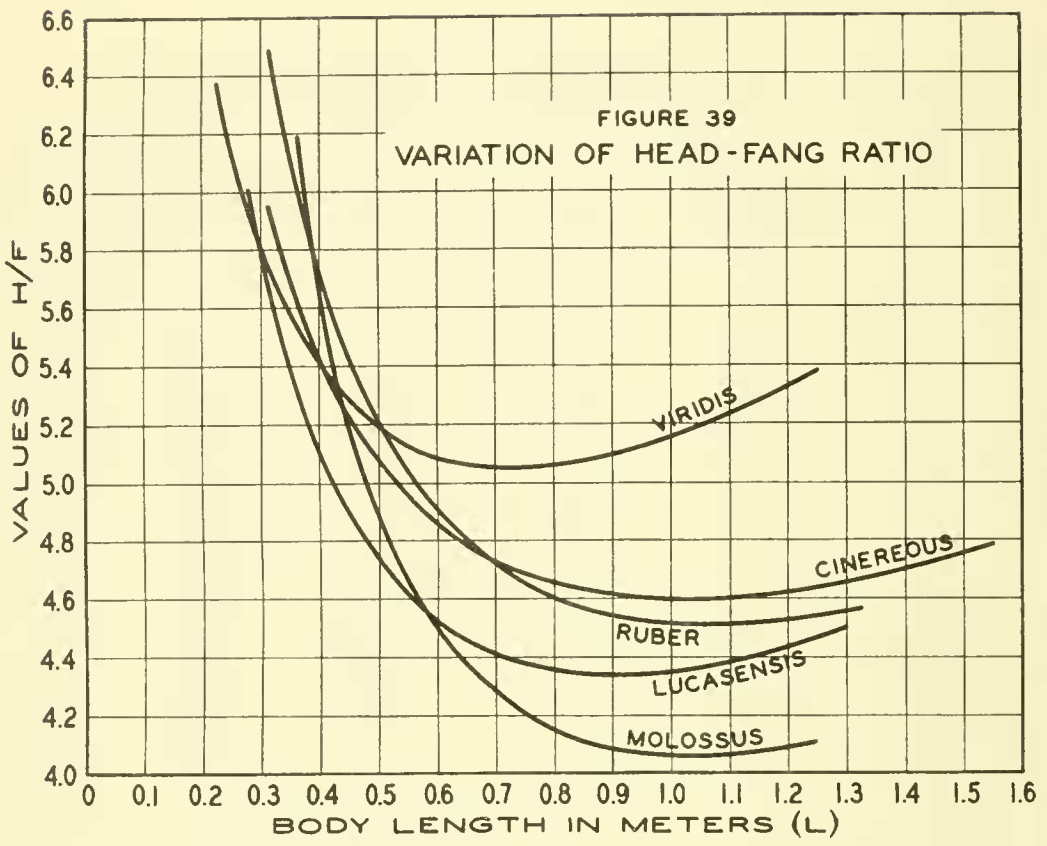
## VARIATION OF H/F WITH H

Head Length in mm.	Values of H/F				
	Molossus	Cinereous	Lucasensis	Ruber	Viridis
20	6.69	5.88	5.87	6.31	5.51
25	5.15	5.17	4.97	5.31	5.19
30	4.56	4.84	4.59	4.86	5.07
35	4.27	4.69	4.42	4.65	5.06
40	4.13	4.62	4.35	4.55	5.12
45	4.07	4.60	4.34	4.52	5.21
50	4.06	4.61	4.38	4.52	5.35
55	4.10	4.66	4.45	4.57	5.53
60	4.16	4.73	4.55	4.64	5.73
65	4.25	4.82	4.67	4.73	5.97
70	4.37	4.92	4.82	4.85	6.24

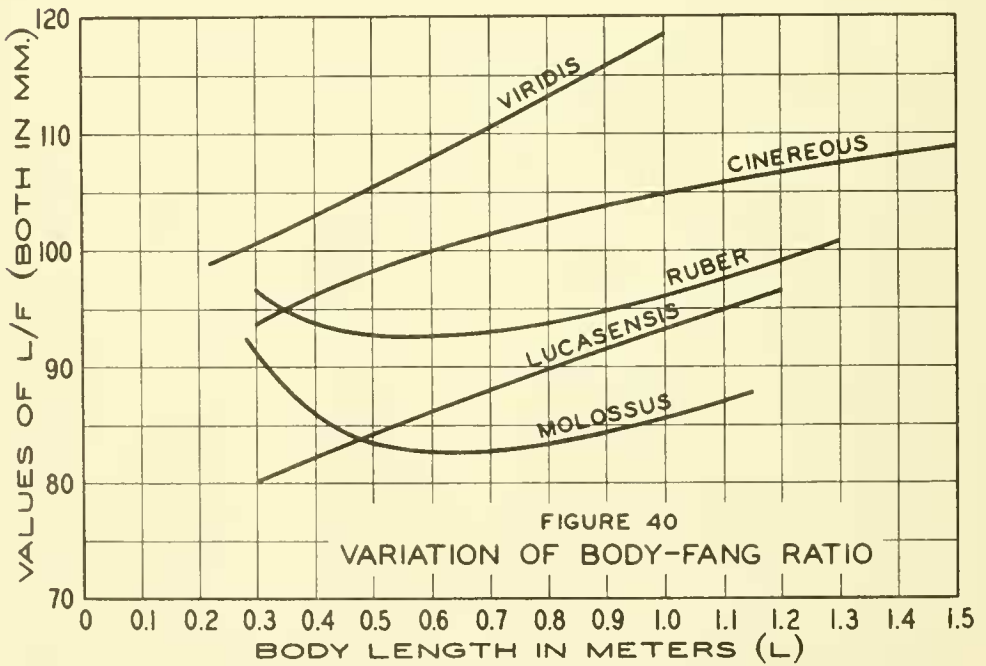
TABLE 28

## VARIATION OF L/F WITH L

Body Length in mm.	Values of L/F				
	Molossus	Cinereous	Lucasensis	Ruber	Viridis
300	91.2	93.8	80.2	96.8	100.7
400	85.7	96.4	82.3	93.7	103.1
500	83.5	98.4	84.3	92.8	105.5
600	82.8	100.0	86.1	92.6	107.9
700	82.8	101.3	87.7	93.0	110.4
800	83.4	102.4	89.5	93.8	113.0
900	84.4	103.6	91.3	94.8	115.7
1000	85.6	104.7	93.0	96.1	118.5
1100	87.0	105.7	94.8	97.5	121.4
1200	88.7	106.6	96.7	99.0	124.5
1300	90.5	107.5	98.6	100.7	127.7
1400	92.5	108.4	100.6	102.5	131.1



42





approximate proportion to body growth, but in the adult stage which is here being discussed, the growth of fangs is more nearly in proportion to head growth. This is also evident from the sample parabolic expressions of the form  $X/Y = dX^k$ , given for the adult range on p. 31, for, if  $k$  is positive,  $H$  or  $L$ , as the case may be, increases more rapidly than  $F$ .

Thus the head size, rather than that of the body, constitutes the better basis of comparison during the adult stage.

### Interspecies Comparisons in Fang Length

In discussing the correlation of head with body length I have pointed out the difficulty of making interspecies comparisons in a character which changes during individual growth (Part V, p. 39). Since a constant ratio is not maintained, one is under the necessity of comparing two regression lines, which can only be done graphically; or of comparing ratios, either at some fixed value of the independent variable, or at some value of that variable related to a specific time of life; e.g., average fully-adult male. None of these schemes is completely satisfactory, being cumbersome in application and involved in exposition. And in the present case the situation is further complicated by the fact that measurements are time consuming and difficult; even if adequate material were available, it would hardly be worth while to make sufficient measurements to locate the regression line of each species with accuracy.

Probably the best scheme of exposition is to plot average adult fang-head (and fang-body) co-ordinates of each species in relation to the regression lines of the five species already fully determined. From their positions with respect to these regressions we can at once tell, at least to the extent of the accuracy of these average points, which species deviate materially from the five species upon which we have concentrated, and the direction of the deviations.

Thus far, such interspecies comparisons as have been made, have been set forth only for the purpose of illustrating the differences between the different types of regression equations, and the errors involved in the use of the abridged forms. We now turn to the differences themselves, first discussing the five species whose regression curves have been determined. The extent of these differences, although inherent in the constants of the equations, and illustrated in Figs. 37 and 38, may be rendered even more explicit by sample tables, setting forth, not only values of  $F$  for different values of  $H$  and  $L$ , but also the changing ratios  $H/F$  and  $L/F$ . These data are presented in Tables 25 to 28. The second degree parabolas have been used in their computation.

Referring first to Table 26, this shows the variation in the fang length of these five species, as the body length varies from 300 to 1400 mm. Of particular interest from the standpoint of interspecies comparisons, is the ratio of the fangs of any two species as the snakes increase in size. Taking viridis and molossus as examples, we find that molossus, at 600 mm., has fangs 30 per cent longer than viridis; at 900 mm. the difference is 37 per cent, and at 1200 mm., 40 per cent. Similarly consider ruber and cinere-

ous. At 600 mm. ruber has longer fangs by 8.0 per cent; at 900 mm. by 9.5 per cent, and at 1200 mm. by 7.6 per cent. We see that these fundamental differences are substantially maintained from adolescence to full growth.

If we feel that these differences are only reflecting head-length differences which we naturally expect the fangs to follow, since they are a part of the head, we return to Table 25, wherein head lengths are varied, to note the corresponding changes in the fangs, and make the same comparisons. At a head length of 30 mm. the molossus fang is 11.1 per cent larger than the viridis fang; at 40 mm. it is 23.8 per cent larger, and at a head length of 50 mm. it is 31.6 per cent larger. In the cinereous-ruber comparison we find that ruber is 2.7 per cent smaller at 25 mm., 1.4 per cent greater at 40 mm., and 1.9 per cent greater at a 55 mm. head length. The closer grouping of the curves in Fig. 37 as compared to Fig. 38 graphically illustrates that, interspecifically, the fangs more nearly follow head than body size.

Thus it is clear that there are interspecies differences which, in some cases, are of considerable magnitude.

We next refer to Tables 27 and 28, which show the trends in the H/F and L/F ratios through the adult ranges of these five species. It is at once apparent, as has already been determined analytically, that there is less difference in the H/F ratio than the L/F, both within a species, and between species, during ontogeny. As the head length doubles in size the change in H/F is usually less than 10 per cent, a condition inherent in the small size of the constant term in the F on H regression equation.

As long as we are sure that H/F remains substantially constant throughout the adult range of a species, we need not be particularly concerned as to the head lengths at which we make comparisons. To the extent that there are intraspecific variations in H/F we must be careful not to compare species of markedly dissimilar adult sizes at the same head length, since we will be comparing the juvenile ratio of the larger with the adult ratio of the smaller.

In Figs. 39 and 40 the data of Tables 27 and 28 are presented graphically. With regard to the first diagram, it should be explained that the H values of Table 27 have been converted to values of L by the use of the constants developed in Table 19 (Part V), since we visualize snake sizes better in terms of their total lengths than in terms of their head lengths. The trend whereby the H/F ratio falls rapidly from the juvenile to the young adult stage, and subsequently rises slightly, is indicated in all five species.

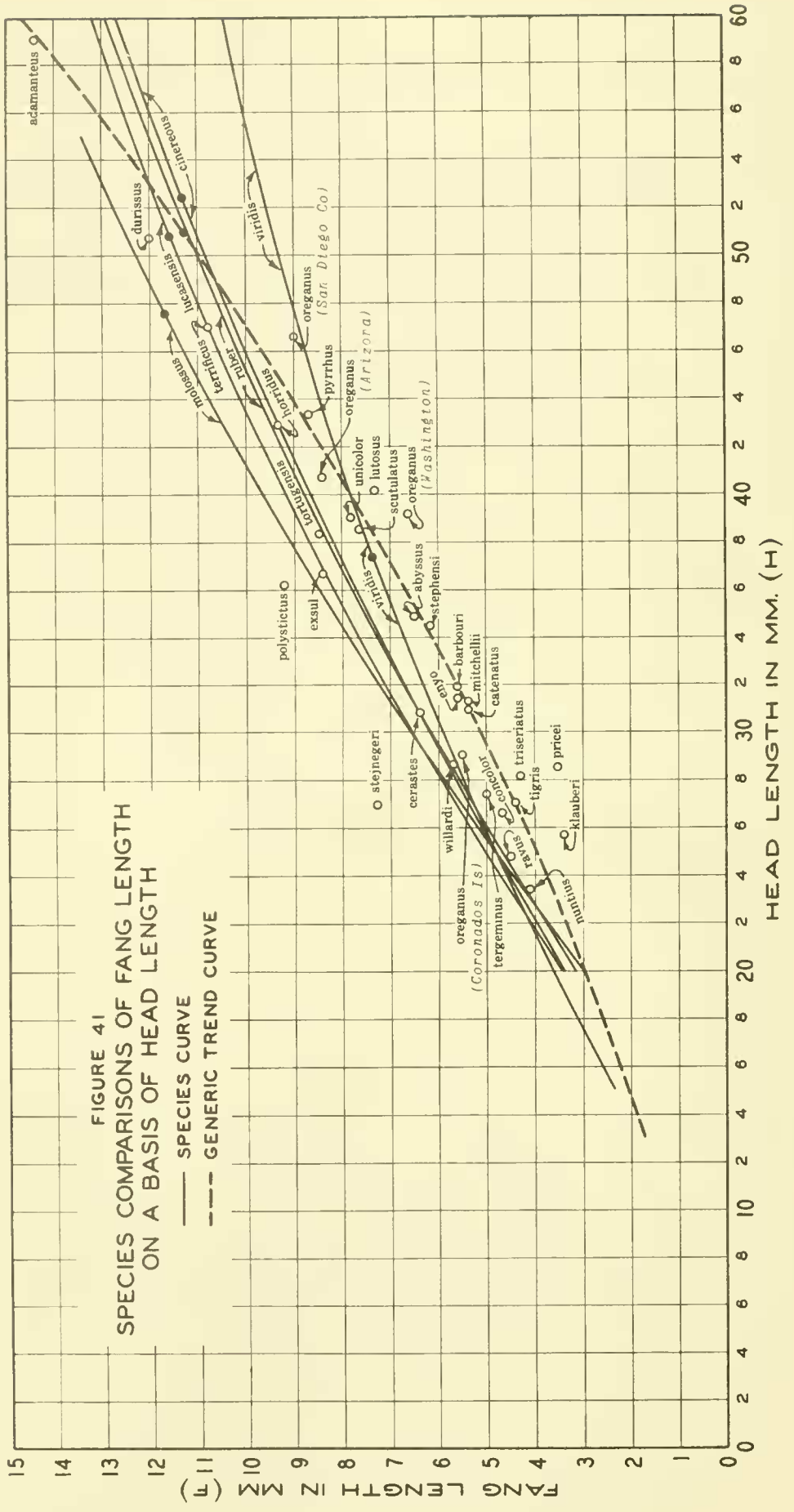
The L/F curves in Fig. 40 show a greater diversity in form. It is to be remembered that the scale is exaggerated. The forms of these curves, in the smaller body sizes, depend greatly on the constant term  $h$  in the equation  $F = fL^2 + gL + h$ . If this term is positive, we have a continuous increase in the L/F ratio, as shown in the cases of viridis, cinereous, and lucasensis; this is not true in molossus and ruber, where  $h$  is negative. In these species, therefore, L/F decreases in the juvenile range, and subsequently increases, as it does in the other species.

It is my opinion that these different types of

## FANG PROPORTIONS: ADULT SNAKES

	Number of Specimens	Body Length Range	Fang Range	Mean L	Mean H	Mean F	Mean L/F	Mean H/F
<i>C. durissus durissus</i>	6	1130-1420	10.8-13.3	1262	50.7	12.0	106	4.27
<i>C. durissus terrificus</i>	2	951-1152	10.1-11.4	1051	45.0	10.8	97	4.18
<i>C. unicolor</i>	1			920	39.0	7.8	118	5.00
<i>C. basiliscus</i>	5	1515-1750	11.7-14.2	1603	63.2	12.7	126	4.97
<i>C. enyo</i>	5	696-854	5.4-5.8	760	31.4	5.6	135	5.59
<i>C. molossus molossus*</i>	44	800-1200	9.6-13.5	1000	47.6	11.7	86	4.07
<i>C. adamanteus</i>	5	1005-1700	13.4-15.8	1214	59.1	14.4	83	4.13
<i>C. cinereous*</i>	52	1000-1700	9.6-12.9	1200	52.4	11.3	106	4.64
<i>C. tortugensis</i>	10	745-1038	6.8-9.4	941	38.3	8.5	112	4.57
<i>C. lucasensis*</i>	270	900-1300	9.9-13.2	1100	50.8	11.6	95	4.38
<i>C. ruber*</i>	100	900-1300	9.5-12.9	1100	51.0	11.3	97	4.51
<i>C. exsul</i>	7	713-940	7.5-9.6	788	36.6	8.4	94	4.37
<i>C. scutulatus</i>	7	812-1035	6.7-8.8	957	38.5	7.6	126	5.14
<i>C. viridis viridis (Platteville)*</i>	590	700-1000	6.3-8.4	850	37.4	7.4	115	5.05
<i>C. viridis nuntius</i>	5	458-540	3.8-4.8	497	23.4	4.1	122	5.76
<i>C. viridis abyssus</i>	5	656-981	5.3-8.4	780	34.9	6.5	121	5.70
<i>C. viridis lutosus</i>	5	793-1173	6.0-8.8	904	40.1	7.3	131	5.49
<i>C. viridis concolor</i>	5	522-735	4.1-5.2	616	26.6	4.7	132	5.75
<i>C. viridis oreganus (Washington)</i>	6	802-1045	6.2-7.5	869	39.1	6.6	132	5.96
<i>C. viridis oreganus (Arizona)</i>	6	850-1065	6.5-9.6	949	40.7	8.4	115	4.93
<i>C. viridis oreganus (S. D. County)</i>	5	855-1140	7.8-9.4	1026	46.6	9.0	113	5.04
<i>C. viridis oreganus (Coronados Isl.)</i>	5	547-683	4.9-6.1	608	29.0	5.5	110	5.22
<i>C. mitchellii mitchellii</i>	7	760-896	5.2-5.7	820	31.2	5.4	151	5.74
<i>C. mitchellii pyrrius</i>	5	826-1114	7.3-10.8	926	43.3	8.7	107	5.01
<i>C. mitchellii stephensi</i>	5	746-885	5.6-7.1	786	34.4	6.2	128	5.59
<i>C. tigris</i>	5	585-778	4.0-4.6	729	27.0	4.4	165	6.11
<i>C. cerastes</i>	5	518-767	5.0-8.1	625	30.8	6.4	98	4.83
<i>C. polystictus</i>	5	531-930	7.0-10.4	825	36.2	9.2	89	3.94
<i>C. horridus</i>	6	912-1162	8.7-10.4	994	42.9	9.3	107	4.61
<i>C. lepidus klauberi</i>	5	520-595	3.2-3.6	555	25.7	3.4	162	7.54
<i>C. triseriatus triseriatus</i>	6	512-621	3.3-4.7	559	28.1	4.3	150	6.60
<i>C. triseriatus pricei</i>	5	525-565	3.3-3.7	550	26.5	3.5	155	7.49
<i>C. steingeri</i>	1			588	27.0	7.3	80	3.70
<i>C. willardi</i>	5	517-579	5.3-6.0	549	28.6	5.7	97	5.16
<i>S. rarus</i>	3	409-632	3.8-5.7	484	24.8	4.5	108	5.61
<i>S. millieri barboursi</i>	5	666-702	5.2-6.3	680	31.9	5.6	121	5.70
<i>S. catenatus catenatus</i>	5	625-787	5.0-5.9	697	30.9	5.4	131	5.78
<i>S. catenatus tergeminus</i>	5	477-625	4.5-5.5	542	27.4	5.0	109	5.51

\* Data from regression lines



trend curves in the correlation of L/F with L are not true specific differences, but result rather from the inadequacy and imperfections of the original measurements; in other words, the differences are not significant. With curvatures in both directions as shown, one may even hazard the guess that the true relationship is of the form  $L/F = a_1L + b_1$ ; that is, the F on L relationship is hyperbolic rather than parabolic. The differences found by applying such curves would be important only in the juvenile range.

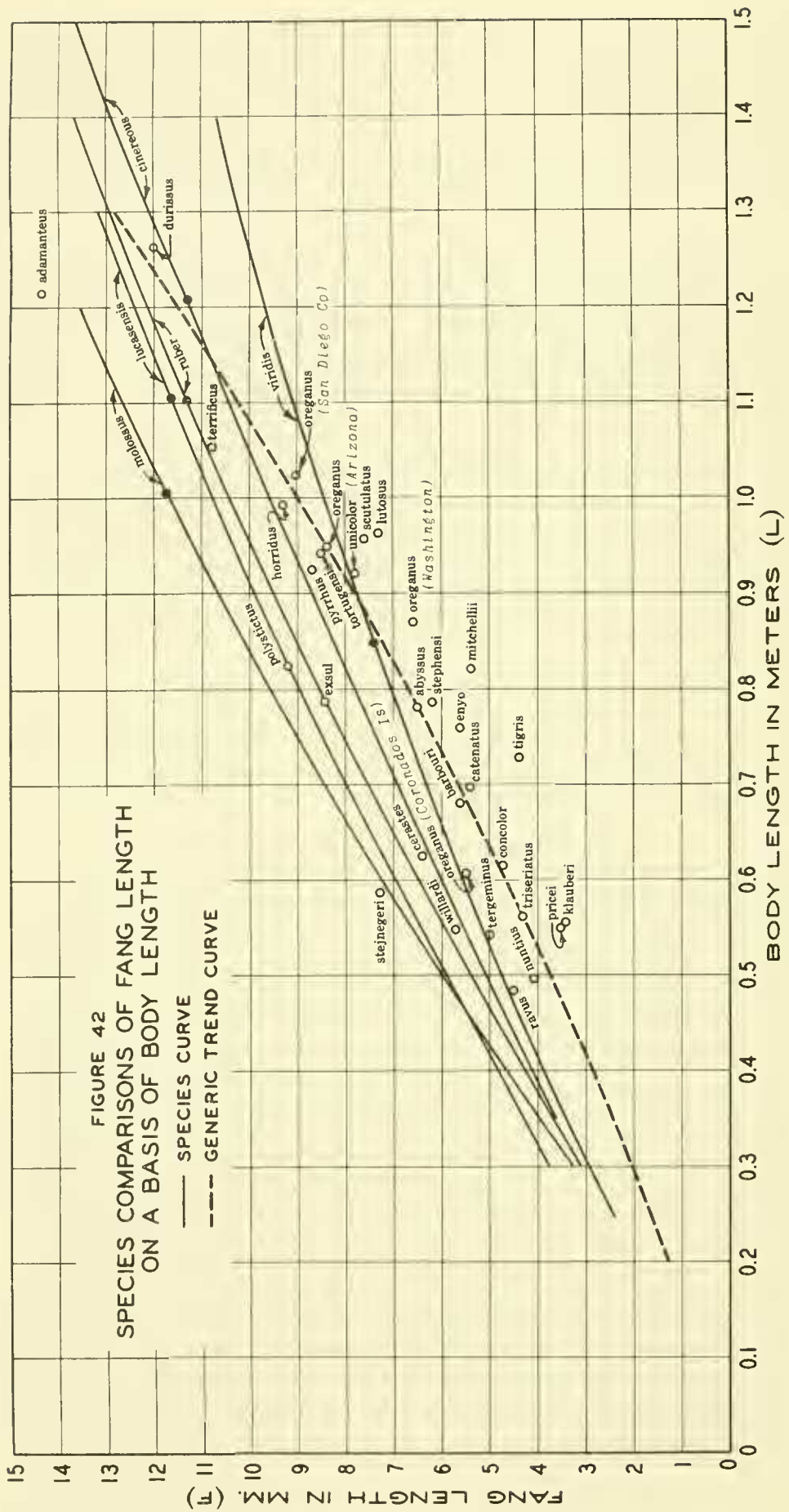
Data showing interspecific comparisons of the rattlers are presented in Table 29. In most cases the statistics are based on the measurements of five adult specimens of each species or subspecies. From these, average values of the H/F and L/F ratios have been computed, it being understood that the ratios were calculated separately for each specimen, and then averaged, rather than dividing the average value of H by the mean of F.

In Fig. 41 the same data are shown by indicating each species as a point, determined by the co-ordinates of the average head and fang lengths, similar treatment being given the body and fang lengths in Fig. 42. In each figure the adult regression lines of the five species previously discussed are also presented; this permits us to orient the other species readily with respect to these five, and to determine at once those which differ essentially from the rattlesnake mode, as represented especially by cinereous and viridis.

In considering these two diagrams, it should be emphasized that the single points which represent the species and subspecies, except those for which complete regression lines have been drawn, are presumed to be based on adult measurements only.

I shall dispose of Fig. 42 temporarily by stating that it merely repeats much that was developed in Part V, with regard to head proportionalities. For we see that tigris, mitchellii mitchellii, and scutulatus have conspicuously short fangs, when compared, on a basis of body length, with the general run of rattlesnake species. But this is only because these species have small heads. Thus we show that, in general, rattlesnakes with small heads proportionate to their bodies, likewise have short fangs on this basis of comparison. This, of course, we might have expected in advance; yet it would not have been impossible for the rattlers to have developed a compensating tendency whereby this handicap might have been balanced by giving these small-headed species unexpectedly long fangs. Such we find not to be the case. So we may say that, to the extent that longer fangs are important in snake-bite cases, snake species with large heads in proportion to their bodies are likely to be the more dangerous, other important variables being equal.

Returning to the more important F on H comparison shown in Fig. 41, we note that, if we consider cinereous to represent the mode of the larger species, and viridis that of the rattlers of more moderate size, we find the rattlers with fangs of unusually large size to be adamanteus, molossus, polystictus, and stejnegeri. The latter species, however, is premised on a single specimen, and therefore is not to be considered conclusive.



It will be observed that most of the subspecies of viridis adhere rather closely to the viridis viridis line, although the desert forms, lutosus, abyssus, and oreganus from eastern Washington, have somewhat shorter fangs. Similarly, ruber, lucasensis, tortugensis, and exsul comprise a well-knit group. Scutulatus, as is the case with many characters, is closer to viridis than to cinereous, notwithstanding its superficial resemblance to the latter.

I would call attention to the manner in which the viridis line curves over and across the cinereous and ruber lines. Viridis, especially the Platteville series from east central Colorado, is a smaller snake than the other two. I am of the opinion that if we had accurate regression lines of the smallest species, we would find them, in turn, curving over the viridis line. This is inevitable unless they have, proportionately, much shorter fangs when juveniles than when adults, a condition not found to exist in the species fully investigated. However, be this as it may, we must remember that constant ratios are represented by straight lines radiating from the origin; and, with all of the smaller species concentrated below a line joining the origin with adult viridis, we reach the conclusion that the adults of small species of rattlesnakes have shorter fangs, proportionate to their head lengths, than larger rattlesnakes. Cerastes and willardi have rather larger fangs, while pricei and klauberi have fangs smaller than the mode of these smaller species.

With respect to the stunted forms, we find that these fall close to the regression lines of their prototypes. Thus, we find tortugensis near the cinereous line; exsul on the ruber line; and Coronados Islands oreganus, and nuntius, on, or near, the viridis line. This indicates that stunted forms have the fang proportionalities of the adolescents of their prototypes, and hence larger fangs than the mode for adult rattlers of non-stunted species of similar head size.

As we study Fig. 41, we cannot fail to observe, in the F on H points, a rather definite trend which has no essential relationship to the regression line of any particular species--a sort of generic regression line of which the variates are the adult averages of the individual species. We might fit a straight line to these data, but in this case it would not pass through the origin. A straight line in F/H appears more appropriate. By elementary curve fitting we find  $F/H = 0.0025H + 0.095$  to fit the scattered points quite well. Thus, our generic regression line becomes  $F = 0.0025H^2 + 0.095H$ . This likewise has been drawn in Fig. 41. Notwithstanding its inexactness, this line may be considered a better guide in judging species deviations from the rattlesnake mode than the ontogenetic line of any single species. It is seen that the majority of species do not deviate from it very greatly. Insofar as our incomplete data indicate, it would appear that stejnegeri, polystictus, exsul, and molossus have unusually large fangs, while klauberi, triseriatus, and the northern oreganus have small.

It is hardly necessary to point out that, in locating the points to be used in deriving a generic relationship of this type, it is important that all of the points represent approximately the same period in the life history of each species (e.g., average fully-adult male), because the ontogenetic curves are not parallel with the generic curve. For example, if our data indicate that a large adult male

ruber has a head length of 40 mm., and a corresponding fang length of 8.8 mm., the point does not fall on our generic curve. However, if the ruber head size which corresponds to the ontogenetic conditions under which the other species were determined, is 51 mm., then the ruber point does fall on the generic curve.

The generic curve obviously shows that a species having a head size twice that of another, has fangs more than twice as long. For example, a species with an adult head length of 30 mm. would have fangs 5.1 mm. long, while one with a head length of 60 mm. would have 14.7 mm. fangs. Thus, with an increase of head length of 100 per cent, the fangs increase 188 per cent. This is not what happens as a growing rattler follows the ontogenetic curve of its species. For example, as ruber grows from a head length of 30 to 60 mm., its fangs increase from 6.17 to 12.93 mm., or only 110 per cent. It may be pointed out that while there may be considerable uncertainties in the generic and ontogenetic curves which I have deduced, particularly with respect to the exact values of the coefficients, there can be no question concerning the directional trends, or the fact that the generic curve is steeper than the ontogenetic curves. That is, there is no doubt that larger species of rattlers have fangs exceeding in length those of the smaller species in greater degree than would be expected from what we know of intraspecies trends, or from a direct proportionality with the other bones of the skull.

Assuming that long fangs are an advantage, if not carried to too great an extreme, we may hazard the guess that these long fangs are possible and necessary to a larger species because it has the weight to drive them in, in a strike, or the muscle to imbed them in a bite, whereas the smaller snake would lack the essential momentum or muscular power. For we have been discussing linear dimensions only; whereas the weight of a rattler increases even faster than the cube of his body length (Part IV, p. 44), and his muscular power at least as rapidly as the square. Thus, the larger snake is provided with the power to drive in a proportionately longer and heavier fang. Again, viewing the venom and fang as a prey-securing mechanism, we must recognize the fact that, if both prey and required venom dosage vary approximately as the third power of the snake's length, the fang should be longer than that involved in a constant ratio with head length. As to the difference in the trend of the ontogenetic curves, these seem to be designed to give to each species its highest F/H ratio (or lowest H/F ratio, see Fig. 39) at the time of most rapid increase in bulk, that is, between adolescence and young adulthood, when presumably, its food requirements are at a maximum.

Although I consider the F on H relationship the most logical and important for study in interspecific relationships, the F on L criterion is also of considerable interest. After all, it is of some value to know that tigris has very small fangs proportionate to its body length, even though this may result from tigris' having a remarkably small head. Hence, we return to Fig. 42. Again, we draw an approximate generic curve in contradistinction to the ontogenetic curves of the five selected species. The situation of the scattered points is found to be fairly satisfied by the equation  $F/L = 3L + 6$ , or  $F = 3L^2 + 6L$ , F being expressed in millimeters and L in meters. Once more, it should



be stated that this very approximate equation refers only to adult snakes, and these of an average adult size rather than to unusually large specimens.

Upon this direct body-length criterion, and making no amendments by reason of disproportionate head sizes which deviate from the rattlesnake mode, we find that the forms with unusually large fangs are stejnegeri, willardi, cerastes, exsul, polystictus, molossus, lucasensis, ruber, and adam-anteus. Species with conspicuously small fangs, compared to their body lengths, are pricei, klauberi, tigris, enyo, mitchellii mitchellii, Washington oreganus, lutosus, and scutulatus.

Again, we find, as when using head length as a basis of comparison, that larger species have fangs longer in proportion to their bodies, than small species. Thus, if two species fall close to the generic curve and one reaches an average adult length of 600 mm. while the other attains 1200 mm., the first will have fangs 4.68 mm. long, while the larger snake will have 11.52 mm. fangs, an increase of 147 per cent, compared with the body increase of 100 per cent. Hence, regardless of head size, it is in general true that larger species have proportionately longer fangs than smaller species.

#### Other Fang Dimensions

Thus far in discussing both intra- and interspecific variations, I have treated them only on a basis of the single dimension F, the distance from the bottom of the upper lumen to the point. As I have stated, this was selected as the dimension most readily and accurately measurable. It is now desired to mention some of the other dimensions and morphological characteristics.

First as to intraspecific variation. A series of some twenty specimens of C. ruber at all ages were studied, measurements being made of the radius and angle of the central curve, and the thickness at the mid-point, these being correlated with F. It was found that the fang does not retain a form of constant proportions, as the individuals of this species grow in size to maturity. The thickness at the mid-point does maintain proportionality up to the time the snake is a young adult, in this particular species, about 900 mm. long. Subsequent to this time there is a more rapid increase in diameter than in length, so that the fangs of the larger snakes are proportionately thicker, heavier walled, and stronger. When it is remembered that the snakes have relatively shorter fangs (proportional to body) in the large sizes, it would appear that the diameter of the tube continues to increase more nearly in proportion to the body length of the snake.

The radius of curvature increases gradually from the smaller to the larger snakes, but apparently reaches a maximum at about 900 mm., subsequent to which there is no further increase in this radius. In this species it is found that this maximum is about 6 mm., which remains constant for fangs between 10 and 14 mm. long. Necessarily this means that the longer fangs have a greater arc of curvature, or longer tangents, since the radius of curvature is not increased as the fangs lengthen.

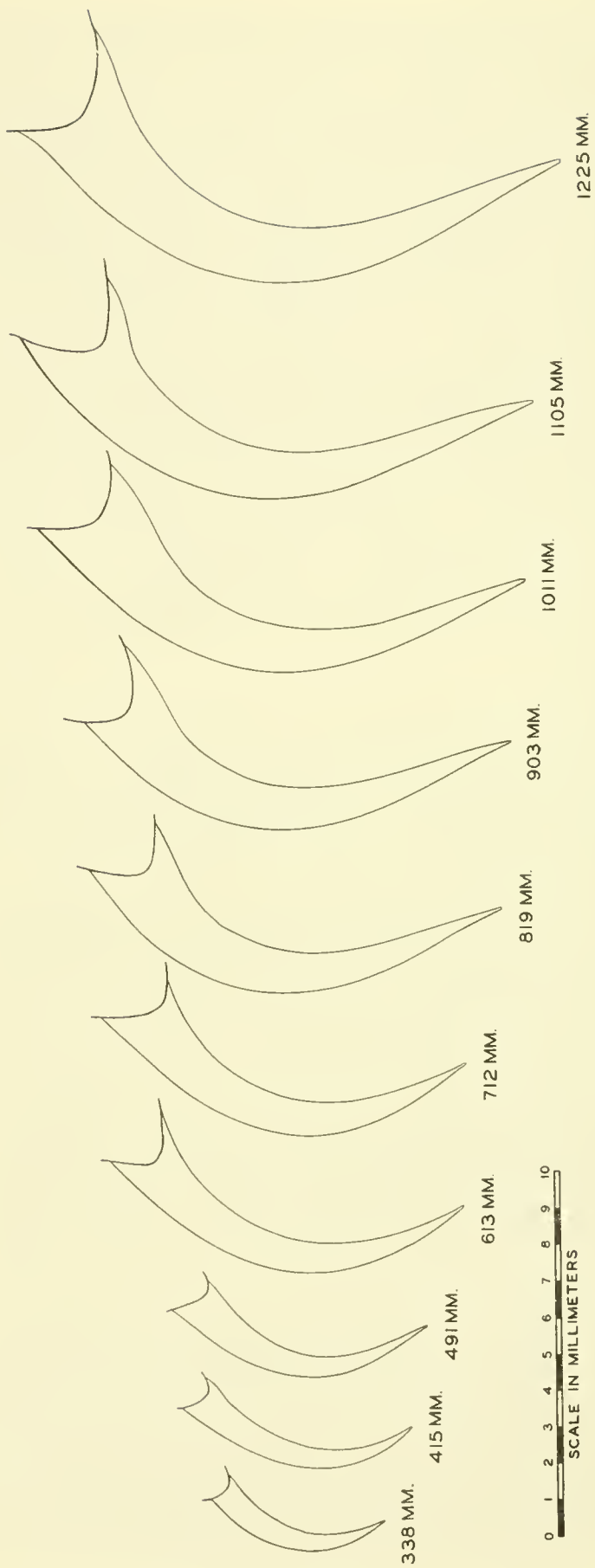


FIGURE 43  
 CHANGE OF FANG SIZE AND SHAPE FROM JUVENILE TO ADULT.  
 SERIES OF CROTALUS RUBER  
 (THE FIGURE BELOW EACH FANG INDICATES THE OVERALL LENGTH OF THE SNAKE IN MILLIMETERS)

The external angle, made by the two terminal sections produced, is difficult to measure with accuracy, especially in the smaller snakes, because of the irregularity of the tangent sections. However, there is a definite indication that this angle does increase as the snakes grow to maturity. For instance, in the juvenile snake having a fang length of 4 mm., this angle, which equals the central angle of the curve, is approximately 65 degrees, while in the fully adult specimens with fangs approximately 12 mm. in length, the angle averages 72 degrees. Thus, the arc of curvature increases with age, and the larger snakes have a relatively more hooked fang. I have not sought to present these ontogenetical changes in the form of equations because the measurements, at best, are not highly accurate and the coefficients of the equations would be of doubtful value. The trends which have been mentioned are, however, unquestioned. For the better illustration of the changes which take place with growth, Fig. 43 has been prepared. This shows a series of ten ruber fangs taken from snakes varying in sizes from about 350 to 1350 mm. at intervals of about 100 mm. The changes in the radius and angle of the central arc are evident.

The best method of indicating some of the species differences in fang shape and proportions is by means of a tabulation of dimensions. Such data are set forth in Table 30, together with Fig. 44, which explains the measurements which are listed.

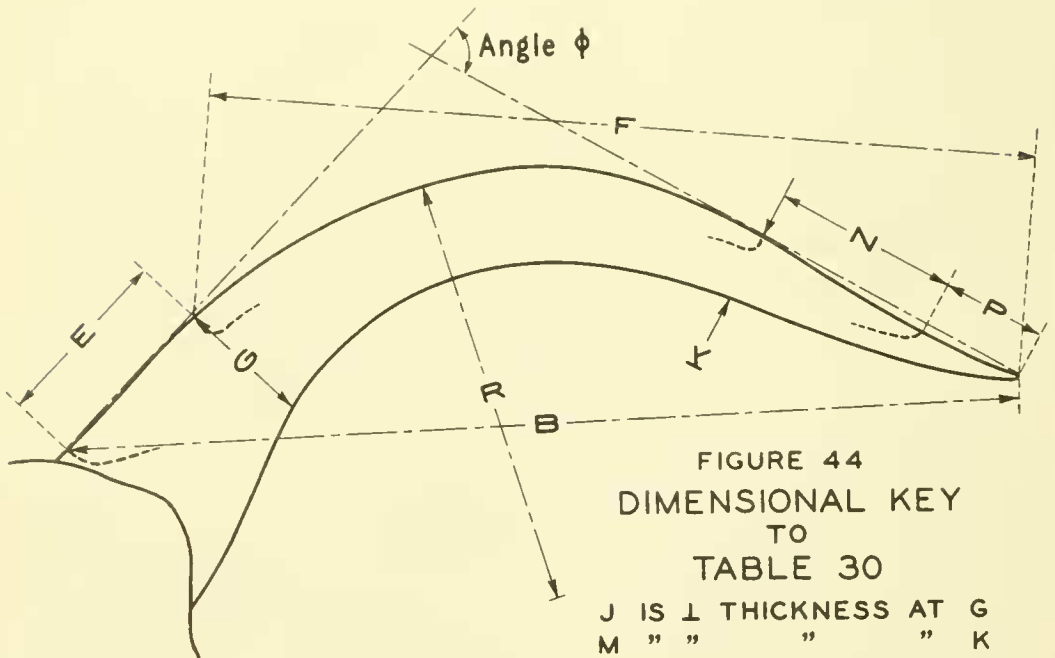
It will be noted that the shape and proportions have a certain uniformity, when allowance is made for variations in F, the total length of the fang.

As previously noted, F is considered the basic length, since it is the dimension which can be most accurately measured. Of the other dimensions the thickness of the fang as given by G, J, K, and N, can be measured with considerable accuracy. E, which represents both the length of the upper lumen and the distance to the edge of the socket, cannot be determined with any degree of certainty, except in the largest fangs, and therefore this is to be taken only as an approximation. The size of the lower aperture, N, is easily determined in some specimens, but not in others, because of the method by which this aperture is formed; the lower end of the slit often merges gradually with the point and therefore the lower terminus is not definitely fixed. The angle also must be considered only an approximation, since the two tangent sections which are presumed to make it are short and somewhat irregular, and therefore their directions difficult of determination. On the other hand, the radius of curvature of the outer edge, which, in the central part of the fang, closely approximates a circular curve, can be determined quite accurately by comparing with arcs of circles of known diameter. It may be noted that the proportionality in the fang is carried even to the point, for the tip is much sharper in the smaller fangs than in the larger, even though the latter may be fresh and therefore unworn.

With reference to the angle, it is observed that the cinereous group, in general, has a greater angularity than the others; followed by the viridis group. Durissus and molossus have conspicuously flat fangs, as is the case also with polystictus. Some of these differences in shape are illustrated in Fig. 45. Small species also tend to have

TABLE 30. SAMPLE FANG DIMENSIONS  
 (Dimensions are in mm./10, except L in mm.)  
 Letters refer to dimensions shown in Figure 44

	Length L	Head H	Fang F	B	E	G	J	K	M	N	P	R	$\phi^*$
<i>C. durissus durissus</i>	1214	524	125	137	18	19	16	8	8	19	10	10	55
<i>C. durissus terrificus</i>													
<i>C. unicolor</i>													
<i>C. basiliacus</i>	1010	650	128	147	24	27	13	13	12	42	10	6	62
<i>C. enyo</i>	737	310	59	65	9	9	8	5	4	12	6	4	63
<i>C. molossus molossus</i>	1123	530	133	150	21	21	17	10	10	37	9	10	55
<i>C. molossus nigrescens</i>	920	490	105	122	16	14	10	8	6	25	10	9	55
<i>C. adamantus</i>	1685	730	171	197	35	47	28	15	14	54	10	9	72
<i>C. cinereus</i>	1630	700	160	179	27	25	21	12	12	35	14	9	82
<i>C. tortugensis</i>	1015	420	84	94	13	15	13	6	6	20	8	5	72
<i>C. lucasensis</i>	1258	590	133	149	18	22	16	12	11	43	12	8	73
<i>C. ruber</i>	1137	555	118	131	17	21	17	9	9	33	9	7	70
<i>C. exsul</i>	831	375	93	105	19	17	13	9	8	28	9	5	88
<i>C. scutulatus</i>	1004	400	87	96	13	16	11	7	6	26	6	6	64
<i>C. viridis viridis</i>	872	375	75	86	15	12	10	6	6	18	8	5	62
<i>C. viridis nuntius</i>	629	274	48	55	9	8	7	5	4	17	5	4	59
<i>C. viridis abyssus</i>	981	430	84	97	19	14	9	7	6	19	7	7	73
<i>C. viridis lutosus</i>	1173	500	88	101	17	17	14	8	7	25	10	6	61
<i>C. viridis concolor</i>	628	261	42	49	8	7	6	4	3	16	5	3	60
<i>C. viridis oreganus</i>	1052	490	93	104	15	18	15	8	8	31	11	6	77
<i>C. mitchelli mitchellii</i>	890	335	57	74	15	13	7	6	5	18	7	3	70
<i>C. mitchelli pyrhus</i>	1114	500	108	126	23	21	16	11	10	41	8	7	71
<i>C. mitchelli stephensi</i>	335	330	71	78	11	16	11	6	6	19	9	5	63
<i>C. tigris</i>	772	280	43	50	9	8	7	5	4	10	5	2½	69
<i>C. cerastes</i>	767	370	81	88	10	14	9	7	6	23	7	5	67
<i>C. polyctictus</i>	905	390	102	116	20	13	11	8	7	21	12	9	44
<i>C. horridus horridus</i>	1162	460	102	118	20	19	12	9	9	30	10	7	70
<i>C. horridus atricaudatus</i>	979	418	100	112	15	16	11	7	7	25	9	7	60
<i>C. lepidus lepidus</i>													
<i>C. lepidus klauberi</i>	693	327	51	59	13	9	8	5	4	15	5	5	58
<i>C. triseriatus triseriatus</i>	520	280	33	39	6	6	5	4	4	15	4	2½	62
<i>C. triseriatus pricei</i>	558	265	36	40	6	7	6	4	4	13	4	4	48
<i>C. atenegezi</i>													
<i>C. willardi</i>	517	275	52	57	7	7	6	4	3	13	5	3	63
<i>S. rarus</i>	409	210	38	43	7	6	5	3	3	9	3	2½	49
<i>S. miharius miharius</i>													
<i>S. miharius barbourn</i>	550	295	54	63	10	9	6	4	3	12	9	5	65
<i>S. miharius streckeri</i>	425	235	37	44	8	6	5	3	3	11	4	3	61
<i>S. catenatus catenatus</i>	787	326	55	62	10	11	8	5	4	15	6	5	69
<i>S. catenatus tergeminus</i>													



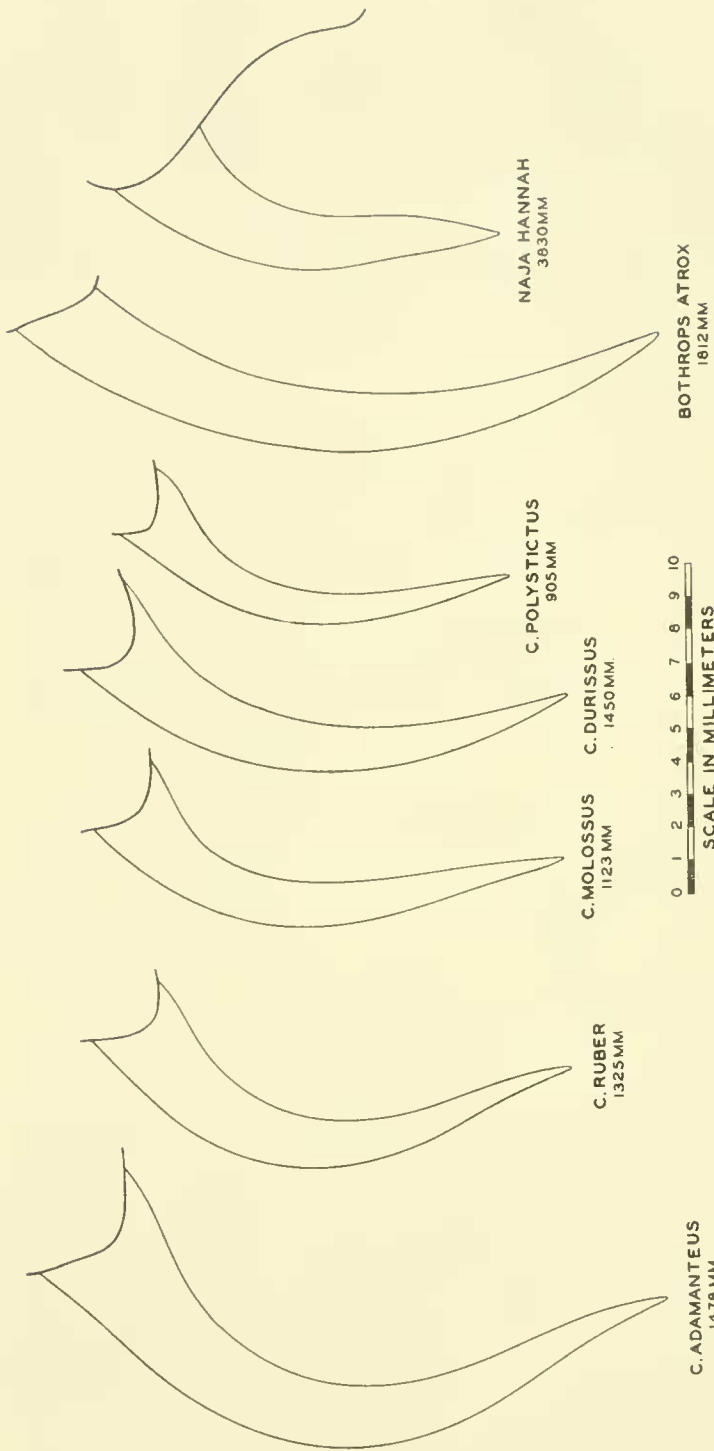
flat fangs, thus showing a generic tendency similar to the ontogenetic trend found in ruber. As to the thickness, an investigation of F/K indicates a tendency for an increased value with the larger snakes, as was evident with growth in ruber. This also is to be expected, for, if the forces (especially transverse) exerted on the fang increase in proportion to the weight of the snake (roughly the cube of the length), then the cross section of the fang must increase more rapidly than would be involved in a mere proportionate increase in linear dimensions, which would increase the cross section only as the square. The structural problem is somewhat similar to that of the cross section of the leg bones of mammals, which cannot bear a constant proportionality, since the compressive strength would increase only as the square of the linear dimensions, while the weight to be supported increases as the cube.

### Miscellaneous Data on Fangs

It should be understood that the statistical data which I have presented apply only to the rattlesnakes, genera Crotalus and Sistrurus. I do not have available adequate series of other genera, either of the pit vipers of the family Crotalidae, or the true vipers, family Viperidae, to determine anything of interest concerning their ontogenetical trends. However, even a superficial survey indicates that generic differences are likely to be considerably greater than interspecific differences, as might well be expected. For example, the fer-de-lance, Bothrops atrox, a common pit viper occurring from southern Mexico to Brazil, has a straighter fang than any rattlesnake. The central curve extends continuously from upper lumen to point, instead of comprising a shorter-radius arc between two tangents, as in the rattlesnakes. A B. atrox fang 18.7 mm. long follows a circular arc with a radius of 17 mm. The radius of the central arc of a C. adamanteus fang of substantially the same length is only 9 mm., for as has been stated, the adult rattler fang comprises a short circular arc between two tangents. Thus the rattler fang is more sharply hooked--it is better designed for biting, and the Bothrops fang for stabbing. The latter somewhat resembles a juvenile Crotalus fang in shape, probably indicating a more primitive form (Fig. 46).

The lateral twist at the point of the Bothrops atrox fang is more pronounced than in the rattlesnake fang, bringing the ridges to the top and bottom. This gives the point, in spite of the presence of the distal aperture, a dagger-like end with the long axis in the plane of the curve. The fang of a large B. jararacussu does not show the ridges exaggerated to the same extent, although the central curve has the characteristic Bothrops arc. The Bothrops fang is somewhat longer than that of C. adamanteus on a basis of body length, but the difference is not great when comparisons are corrected for the sharp bend in the rattlesnake fang.

Another neotropical pit viper, the bushmaster, Lachesis muta, is said to have very long fangs; however, whether these are out of proportion to its body length I cannot say; the bushmaster is the longest (but not the heaviest) of the venomous snakes of the Americas, reaching a length of 12 feet. The African Gaboon Viper, Bitis gabonica, an extremely heavy-bodied snake belonging to the family Viperidae, is said to attain fangs closely approach-



**FIGURE 4S**  
**DIFFERENCES IN FANG CURVATURE**  
*(The dimensions under each species indicate the length of the snake over-all.)*

ing 2 inches in length.\* Atractaspis, another African genus of the same family, although not a large snake, has exceedingly long fangs in proportion to either head or body size.

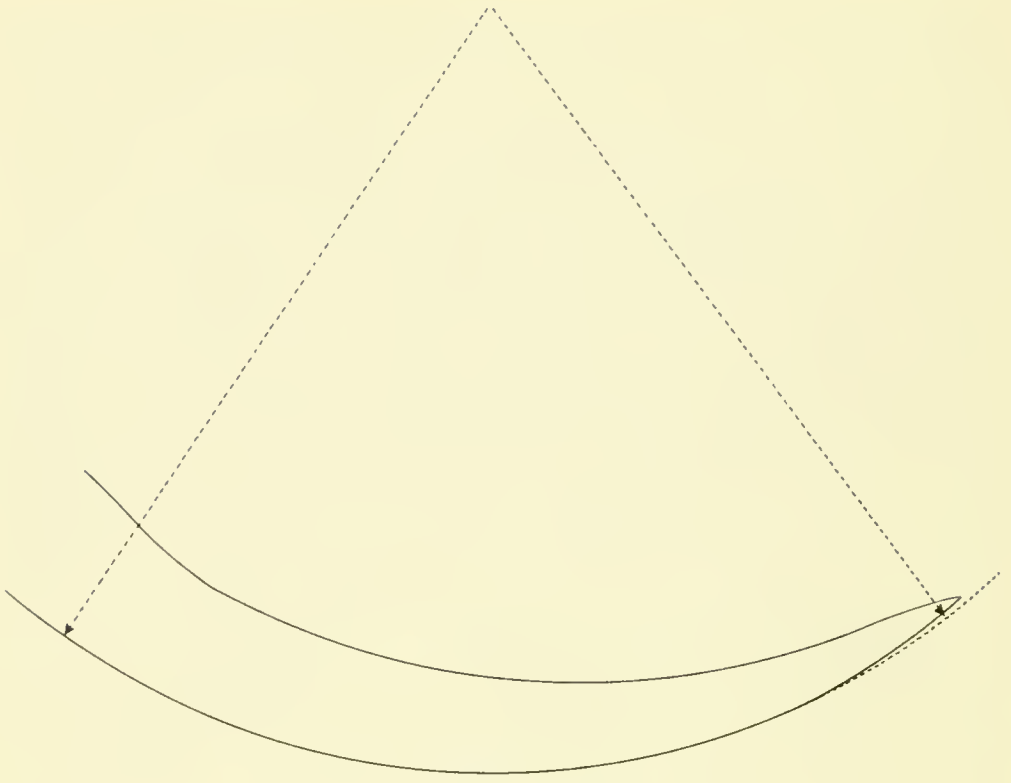
Of course, fang length, while of importance in the consideration of any problem involving snake bite, is outweighed by other factors, especially venom toxicity, venom yield, and aggressiveness of disposition. Thus the snake which is generally agreed to be the most dangerous in existence, the king cobra, Naja hannah, belonging to the family Elapidae, has relatively short fangs. The snakes of this family differ from the viperine snakes in having permanently erect fangs, for the maxillary does not rotate. Compared to the long viperine fangs, which fold back against the roof of the mouth when not in use, the elapine fangs are heavy, with less attenuated points. The reinforcing ridges at the points are on the sides, instead of above and below as in Crotalus. The fangs of a king cobra 3830 mm. (12-1/2 feet) long are found to have an F length of 10.1 mm. and an over-all length of 12.2 mm. The head length is 91.5 mm. Thus this 12 foot snake has fangs only as long as a C. ruber with a body length of 950 mm. (37 inches). The suture or weld in the cobra fang is less perfectly made than in the viperine fangs; it can be felt with a needle point throughout its length. However, the central canal is well sealed. In the specimen before me one fang is in the inside, and one in the outside maxillary socket, indicating that synchronism in replacement is not the rule in the elapine snakes any more than in the rattlers.

The extreme size of fangs reached in the rattlesnakes may be of interest. I have not had the opportunity of measuring the fangs of any very large specimens of C. adamanteus, the largest of the rattlers, and the heaviest of all venomous snakes. The largest available to me have been a series some 1600 mm. (5 ft. 3 in.) long, with fangs having an F length of about 17 mm. (11/16 in.). Calculations lead us to expect that a 2440 mm. (8 ft.) specimen would have fangs about 22 mm. (7/8 in.) in F length. This would make the over-all length, to the distal edge of the maxillary, about 27 mm. (1-1/16 in.). Thus rattlesnakes do not by any means have the largest fangs found amongst the venomous snakes; the African vipers of the genus Bitis probably exceed all other snakes in this characteristic.

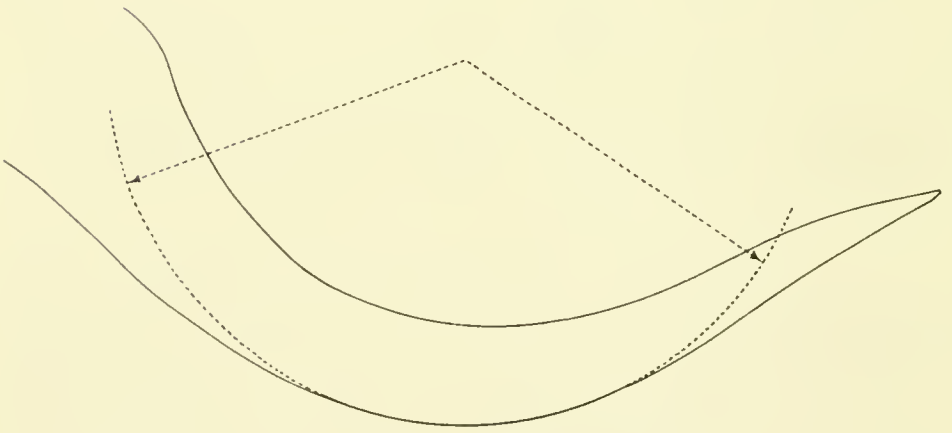
Occasionally a physician, in the treatment of rattlesnake bite, will be aided by having some knowledge of the depth of penetration of the fangs. For example, this may be of value in determining the depth for incision, in the drainage method of treatment. Rough estimates are possible from the separation of the fang marks; however, I trust it will be understood that the results cannot be considered more than guesses. The conditions of snake bite are so variable, and the looseness of articulation of the fangs so considerable, that accuracy is not to be expected. I would say that with such typical species as cinereus, viridis, and oreganus, the depth may approximate 75 per cent of the separation; in adamanteus, ruber, lucasensis, and molossus, 80 to 90 per cent. Only in the Mexican form, polystictus, with its long fangs and slim head, would the depth be likely to equal the separation of the fang puncture marks.

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\* R. S. Pitman, A Guide to the Snakes of Uganda, 1938, p. 270



*Bothrops atrox*



*Crotalus adamanteus*

FIGURE 46  
GENERIC DIFFERENCES IN CENTRAL ARC



## Acknowledgments

In this investigation of rattlesnake fangs, I have received valuable assistance from many individuals. The figures have been prepared by Norman Bilderback and Leslie C. Kobler. Fang measurements were made by Lawrence H. Cook, Robert Hoard, and Charles Shaw. Skull dissections were undertaken by James Deuel and Norman Bilderback. In the statistical computations I was greatly aided by Mrs. Elizabeth Leslie, Alice Klauber, and Philip A. Bailey. C. B. Perkins has made valuable criticisms of the manuscript. To all I am deeply grateful.

## Summary and Conclusions

1. The method of fang replacement in the rattlesnake is described. There are two maxillary fang-sockets on each side of the head and these are used alternately as the location of the active fang on that side. The next replacement fang always lies behind the vacant socket; in this it becomes anchored by the solidification of a bony pedestal when the time for replacement arrives. Replacement is periodical, regardless of whether a functional fang has been damaged. Replacement on the two sides of the head is not synchronous. At the time of replacement there is a short period of overlap during which the new fang, and the one which will shortly drop out, are both functional. Fang change is so frequent that only during the period of most rapid growth in the largest species can a difference in length be detected between a fang and its next replacement.

2. A typical replacement series of fangs is described. There are usually about eight fangs in such a series, lying in a staggered order above and behind the maxillary sockets, one complete series on each side of the head. They are in a graduated order of completeness, from the first replacement, which is complete except for the mounting pedestal, to the last of the series which is a mere bud. In development, as shown by the several members of a series, the portion of the fang comprising the lower or discharge aperture is formed first. The point is next completed, after which the upper tubular section is gradually extended until the full length is reached. Hardening is gradual, the older parts being hardened first. The last part to be formed and hardened is the striated pedestal upon which the fang is mounted in the socket.

3. The completed fang has a suture on the front between the apertures, like a longitudinal weld in a pipe. This suture is so perfect that it can be seen but cannot be felt with a sharp point. The fang, which is quite brittle, when fractured does not crack along the suture. However, in the softer development stage, a fang will always split evenly along the suture. The individual fang is not formed by rolling a flat member, as might be expected from the presence of the suture. On the contrary, it is formed as a tube.

4. The shape of the fang is described and illustrated. It is essentially comprised of an inner tube (the venom duct) and an outer tube, separated posteriorly by a crescent-shaped pulp cavity which extends into the point. At the front along the suture the two tubes are joined and homogeneous. Where they are separated the inner tube is thinner-walled, and is softer than the outer.

5. The mechanism whereby the maxillary is rotated so that the fang can be translated from a resting position against the roof of the mouth, to a striking or biting position perpendicular thereto, is described. The fangs are particularly well designed for biting, rather than merely for striking. They seem better designed for effectiveness on small than on large objects.

6. A convenient criterion for measuring fang length is developed. Studies are made of individual fang variation and sexual dimorphism. The latter, if present, is so small that it can be neglected. The coefficient of variation of individual fang dispersion, based on four fully-formed fangs per snake, is probably less than 1-1/2 per cent.

7. Studies of intraspecific correlation between the length of the fang and that of the head indicate that the variation closely follows a second degree parabolic curve, the coefficients of which are determined for five example species. A curve of the same type also describes the fang-body correlation. Simple parabolas and straight lines are found to be reasonably accurate for short length-ranges, for example, the adult range.

8. In general, the fang length has a substantially constant ratio with body length during the juvenile stage, but subsequently grows proportionately slower than the body. In comparison with head length, the fangs increase at a more rapid rate than the head in the juvenile stage, at the same rate when young adults, and at a less rapid rate in the fully adult stage.

9. The correlation studies show a considerable dispersion about the regression lines. A cross section of the dispersion surface is found to be substantially normal. The coefficient of variation in such a cross section is about 5-1/2 to 8 per cent. Ontogenetically, the dispersion is substantially constant on a percentage rather than on an absolute basis.

10. While the coefficient of correlation with body length over-all is somewhat higher than on a basis of head length, the latter offers the better datum for taxonomic or phylogenetic comparisons, since the head-length to fang-length ratio is more nearly constant during the important adult stage than is the other ratio. There

are extensive interspecies differences on either basis.

11. Interspecific charts are presented showing the species differences. Group relationships are evident, thus verifying phylogenetic relationships founded on other characters. Stunted forms have the fang proportionalities of the adolescents of their prototypes, and hence have proportionately large fangs.

12. There is a definite indication of a generic relationship which differs from the ontogenetic curve of growth within a species. In the adult stage, larger species of rattlers have proportionately longer fangs than the smaller species in the same stage. These trends seem to be related to the physical stresses which the fangs must meet.

13. Other morphological characteristics of the fangs are discussed and charted. With respect to ontogenetic variation, larger fangs are found to be thicker walled than would be expected on a basis of constant proportionality. The radius of curvature of the central arc remains constant after the young adult stage. The degrees of curvature involved in the central arc increase with age, so that older snakes have more hooked fangs.

14. Interspecific differences in form are also investigated. Some species are found to have flatter fangs, while others have a greater curvature. A few generic differences are pointed out.